Bull. nat. Hist. Mus. Lond. (Geol.) **51**(2):89 Issued 30 November 1995

Palaeontology of the Qahlah and Simsima Formations (Cretaceous, Late Campanian-Maastrichtian) of the United Arab Emirates-Oman Border Region

CONTENTS

Preface

M.K. HOWARTH

Department of Palaeontology, The Natural History Museum, London SW7 5BD

The eight papers in this volume describe the Upper Cretaceous macrofossils collected by members of the Palaeontology Department of The Natural History Museum and others during their investigations of the Qahlah and Simsima Formations in the United Arab Emirates-Oman mountain area. The photograph above shows the spectacular unconformity at an exposure 1 km south of Jebel As-Safir in the Jebel Huwayyah area, between the sub-vertical Jurassic cherts of the Haliw Formation, and the overlying near-horizontal carbonate sequence of the late Upper Cretaceous Simsima Formation. The Haliw Formation is part of the Hawasina Group that contains mantle-derived ophiolites elsewhere, and is an obducted nappe complex that was thrust into position during the mid-Upper Cretaceous and forms the basement beds below the unconformity. The rudist-rich Upper Campanian/Lower Maastrichtian Qahlah Formation is absent at this locality, being overlapped by the Simsima Formation which lies directly on the truncated beds of the basement. The Simsima Formation yielded most of the other macro-fossils, including 45 species of echinoids belonging to 33 genera, which is one of the most diverse assemblages of echinoids in the Upper Cretaceous known anywhere in the world. The field collecting and work were made possible by a continuing grant to Peter J Whybrow, The Natural History Museum, from the Abu Dhabi Company for Onshore Oil Operations, and in particular we would like to thank Dr Terry Adams, Mr David Woodward and Mr Kevin Dunne, successive General Managers of ADCO for their support and encouragement. In addition we thank Mr Nabil Zakhour, Head of Public Affairs and Dr Jose E de Matos, Senior Geologist, ADCO, for their sustained assistance. The ADCO grant for research in and around the Emirate of Abu Dhabi forms part of the Natural History Museum's '*Global Change and the Biosphere*' research theme.

Bull. nat. Hist. Mus. Lond. (Geol.) **51**(2):91-119 Issued 30 November 1995

Late Cretaceous carbonate platform faunas of the United Arab Emirates-Oman border region

A.B. SMITH, N.J. MORRIS and A.S. GALE

Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.

W.J. KENNEDY

Department of Earth Sciences, University of Oxford, Parks Road, Oxford OX1 3PR, U.K.

CONTENTS

SYNOPSIS. The stratigraphy and macrofauna of the Qahlah and Simsima Formations is described for 14 sections along the western margins of the North Oman Mountains between Al Ain and Al Dhaid. These are the earliest autochthonous deposits following emplacement of the Semail ophiolite complex and are dated, on the basis of ammonites, inoceramid bivalves and echinoids, as latest Campanian to Maastrichtian in age. Deposition over a deeply weathered surface of ultrabasic rocks commenced with nearshore conglomerates, grits and cross-bedded sands which, in places, have an *in situ* bivalve fauna. Clastic input was abruptly terminated by a sea-level rise and replaced by carbonate deposition in the early Upper Maastrichtian. The basal carbonate bed is composed of coarse shoreface reefal debris formed during rapid transgression. This is overlain by a highly fossiliferous series of muddy carbonate sands deposited in shallow water around wave-base. There is indirect evidence for algal stands from the associated macrofauna, and level-bottom thickets of corals/rudists are present. Upper beds are well-washed carbonate sands rich in larger benthic foraminifers but with few macrofossils that were deposited in broad subtidal flats. In places these are overlain by deeper shelf-basinal marls. Bed by bed faunal lists for each section are provided.

INTRODUCTION

The Oman Mountains form a prominent arcuate range along the northeastern corner of the Arabian Peninsula. Their geological history is complex, but work by Glennie *et al.* (1974), Glennie (1977), Hughes-Clarke (1988) and contributers to Robertson *et al.* (1990) has done much to improve our understanding of this region. The rocks forming the Oman Mountains can be divided into seven major geological units, ranging in age from late Proterozoic to early Tertiary. Of direct interest here are the Hawasina Group, the Semail Nappe and the Maastrichtian to early Tertiary autochthonous marine clastics and carbonates. The Hawasina Group is formed of tectonic slices of Permian to mid-Cretaceous sedimentary sequences deposited over the ocean floor and continental slope of the Arabian continent. They were obducted onto the continental margin of the Arabian platform during the Upper Cretaceous. The Semail Nappe represents a massive slice of former oceanic crust, generated by subduction-related spreading during the Cenomanian-Turonian and emplaced before the Upper Campanian. Both are overlain by marine sediments of Maastrichtian to Palaeocene age. Initially these beds were deposited around the newly emergent margins of the Arabian shield, following the obduction event. Later, a broad carbonate platform formed over the region as it subsided. Only remnants of this once widespread succession now remain, forming small jebels along the western margins of the Oman Mountains.

The late Cretaceous to early Palaeocene rocks are conventionally divided into three units (Skelton *et al.* 1990), which are, from bottom to top:

1. The **Qahlah Formation** – a marine clastic sequence of sands and conglomerates of late Campanian or early Maastrichtian age.
2. The **Simsima Formation** – a platform carbonate sequence of Maastrichtian age.
3. The **Pabdeh Group** – a basal limestone conglomerate of reworked Simsima Formation with an erosive base, of

presumed early Palaeocene age, overlain by thin-bedded basinal marls of late Palaeocene age.

Until recently little was known of the fauna of the late Cretaceous rocks of this region. The first published account of Cretaceous fossils was that of Carter (1852), who described late Cretaceous sediments of the Hadramaut region of south-east Oman. Parts of the fauna collected by Carter were described by Duncan (1865) and are Cenomanian in age. Lees (1928) gave the first authoritative account of the geology of the Oman Mountains and provided much new palaeontological data. He described late Cretaceous faunas from several localities, including Jebel Bu Milh ('Jabal al Milah in Wadi Sharm'), where he recorded and described 39 taxa of gastropods ('the product of an hour's collecting'). Clegg (1933) also described a small number of late Cretaceous species from Oman, but without stratigraphic details.

In the past few years there has been renewed interest in the geology and palaeontology of the late Cretaceous deposits around the fringes of the Oman Mountains. The regional setting of these deposits was outlined by Alsharham & Nairn (1990, 1994), who also described lithofacies and listed microfauna for type sections. The late Cretaceous stratigraphy and faunas from the south western Oman Mountains (Dhofar region, Oman) were studied by Platel & Roger (1989), Roger *et al.* (1989) and Roman *et al.* (1989). Late Cretaceous ammonites, echinoids, foraminifera and calcareous algae were described from the central Oman Mountains (Smith *et al.* 1990, Kennedy & Simmons 1991). To the north, along the United Arab Emirates-Oman border region, Skelton *et al.* (1990) studied key late Cretaceous sections from both a sedimentological and palaeontological standpoint. They published lithostratigraphic sections and faunal lists for these sections, with particular emphasis on the rudist bivalve faunas, from which they were able to provide the first detailed assessment of late Cretaceous palaeoenvironments for the region, demonstrating that the carbonate succession recorded a variety of facies ranging from intertidal to shelf basinal settings. Finally, there are a series of papers documenting part of the diverse echinoid fauna (Ali 1989, 1992a,b) and a few of the molluscs and corals from this region (Ghalib, 1989, 1990; Metwally 1992).

Our interest in the faunas of this region began in 1984, when Dr. S. Nolan (then at the University of Swansea) and Dr. P.W. Skelton (Open University) brought back their collection of late Cretaceous fossils for identification. This, together with material brought to the Natural History Museum for identification by amateur collectors (notably, Mrs Valerie Chalmers), alerted us to the importance of the Maastrichtian faunas of the western fringes of the Oman Mountains. In April, 1991, A.B. Smith carried out a preliminary survey of some late Cretaceous fossil localities along the Oman-United Arab Emirates border. The echinoid fauna proved to be exceedingly rich and also remarkably well-preserved, and without doubt represents the most important Maastrichtian Tethyan echinoid fauna yet known.

During this initial survey it became rapidly apparent that the molluscan and coral faunas were also exceedingly rich and likely to be of equal importance, both in terms of new taxa and their significance for understanding late Cretaceous

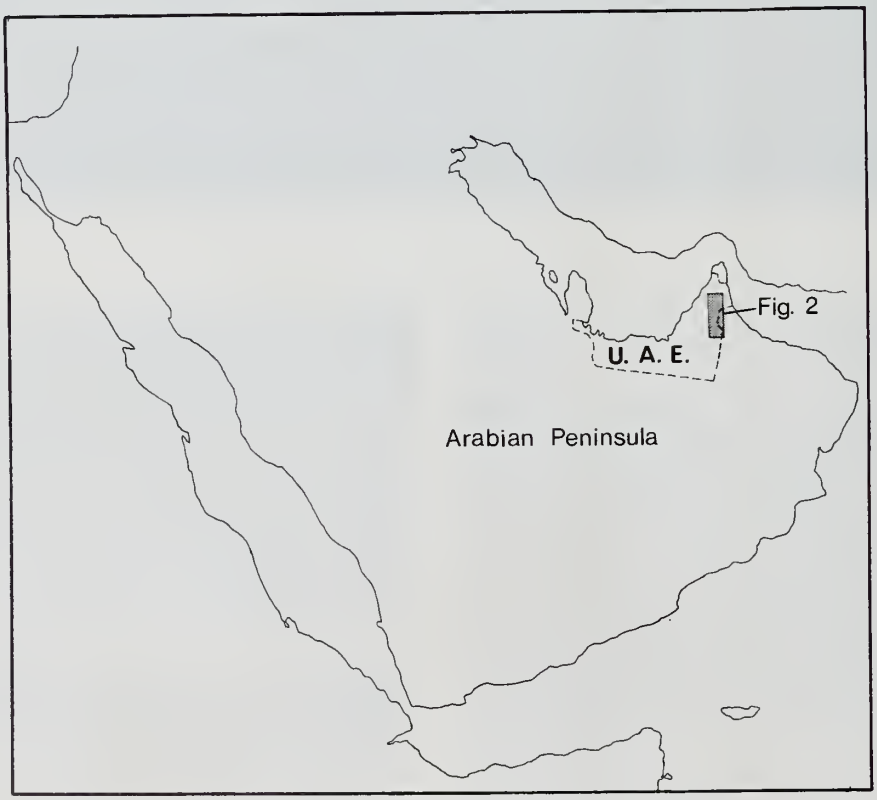


Fig. 1 Map of the Arabian Peninsula showing the area of study.

benthic community structure. Indeed, the small collections brought back to London for examination here by relevant experts generated considerable interest. Consequently a second expedition was mounted to study the entire macrofauna from these important sections and to investigate the lithofacies and palaeoenvironments in more detail. In January, 1992 three of us (ABS, NJM, ASG) spent two weeks exploring, logging and collecting from the late Cretaceous outcrops that form the western margins of the Oman Mountains along the United Arab Emirates Oman borders region. It is the results of these two bouts of fieldwork that form the subject of the following papers.

STUDY AREA

Our study area lies along the border between the United Arab Emirates and the Sultanate of Oman (Fig. 1). Outcrops in this region comprise small, generally outlying jebels along the western fringes of the Oman Mountains. Collection and logging was carried out at eight sites ranging from Jebel Huwayyah in the south to Jebel Faiyah in the north (Fig. 2). Sections were measured at each jebel and macrofauna collected or noted bed by bed. Details of the outcrops studied are as follows:

1. Jebel Huwayyah (Figs 2, 3). Two sections were logged and their faunas collected systematically.
Jebel Huwayyah, section 1. Southeastern corner of the U-shaped Jebel immediately to the north of the dirt track and about 3 km SE of the northwestern corner of the jebel, 10 km NE of Al Ain, United Arab Emirates. Map reference: Buraymi Sheet 1:100,000 NG–40–140; grid reference 842,878.
Jebel Huwayyah, section 2. Western face of the eastern limb of the jebel approximately 2 km SSE of the northwestern corner of the jebel, 10 km NE of Al Ain, United Arab Emirates. Map Reference: Buraymi Sheet 1:100,000, NG–40–140; grid reference 823,877.

2. Jebel Bu Milh (Fig. 3). Two sections were studied in detail.
Jebel Bu Milh, section 1. Western face of a prominent ridge at the northwestern tip of the jebel, 10 km NW of the village of Mabdah, Oman. Map reference: Buraymi Sheet 1:100,000 NG–40–140; grid reference 895,075.
Jebel Bu Milh, section 2. Southeastern corner of a prominent knoll, isolated from the main jebel at its northern end, some 10 km NW of Mabdah, Oman. Map Reference: Buraymi Sheet 1:100,000 NG–40–140; grid reference 906,075.

3. Jebel Rawdah (Figs 2, 4B). Six sections were examined in detail and a further two briefly investigated but not logged or systematically sampled. Logged sections are as follows:
Jebel Rawdah, section 1. Slope and cliff at the eastern end of the northern flank of a valley some 50 m east of the head of the valley, 3 km east of quarry weigh-bridge and site office, Jebel Rawdah, east of Al Madam, United Arab Emirates. Sumayni sheet NG–40–14A 1:100,000; grid ref. 925,528.
Jebel Rawdah, section 2. Slope and cliff on northern side of Jebel Rawdah, about 2 km east of quarry weigh-bridge and site office, Jebel Rawdah, east of Al Madam, United Arab Emirates. Sumayni sheet NG–40–14A 1:100,000; grid ref. 913,544.
Jebel Rawdah, section 3. Slope and cliff on south side of valley from 200 to 600 m east of the head of the valley, about 3 km east of quarry weigh-bridge and site office, Jebel Rawdah, east of Al Madam, United Arab Emirates. There were three measured sections, labelled from west to east a, b, and c. Sumayni sheet NG–40–14A 1:100,000; grid refs 932,528 (section 3a): 928,527 (section 3b) and 927,527 (section 3c).
Jebel Rawdah, section 4. Slope and cliff at the eastern end of the northern flank of a valley, 600 m east of the head of that valley, 2.5 km east of quarry weigh-bridge and site office, Jebel Rawdah, east of Al Madam, United Arab Emirates. Sumayni sheet NG–40–14A 1:100,000; grid ref. 928,531.

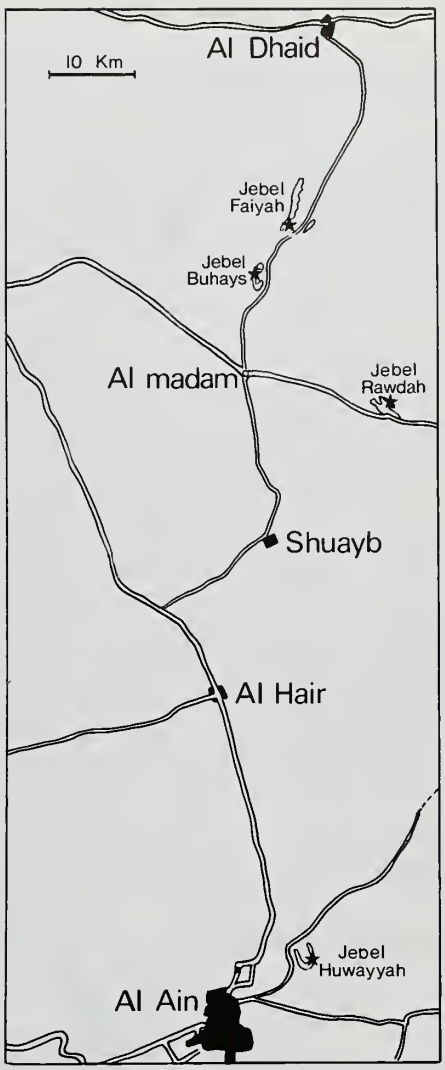


Fig. 2 Locality map showing the position of the four major jebels studied (asterisked) where there are important outcrops of late Cretaceous sediments. For regional placement see Fig. 1.

4. Jebel Buhays (Figs 2, 4A). Two sections were logged and their faunas systematically collected. A third section (2), exposing the lowest beds of the sequence was impossible to

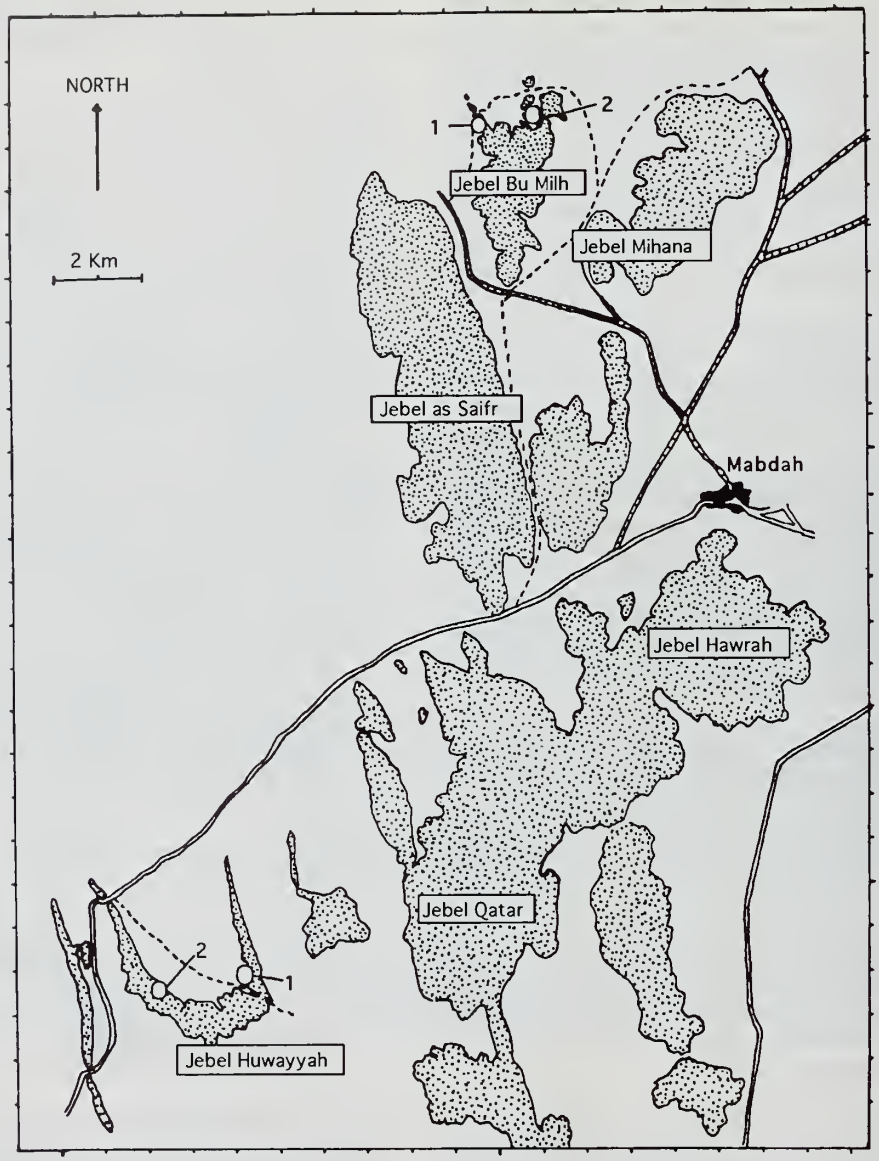


Fig. 3 Detailed locality map for Jebel Huwayyah and Jebel Bu Milh. 1, 2 = studied sections. For regional placement see Fig. 2.

log, but collections were made from the scree slope.

Jebel Buhays, section 1. East face of the most northerly hill forming Jebel Buhays, 4 km north of Al Madam, United Arab Emirates. Dhayd Sheet 1:100,000, NG–40–107; 780,681. A second section 300 m to the south and forming another small hill was also examined and collected from, but no detailed section was made.

Jebel Buhays, section 2. Scree slope at the southwestern corner of Jebel Buhays, 4 km north of Al Madam, United Arab Emirates. Dhayd Sheet 1:100,000, NG–40–107; grid ref. 779,668. No measured section could be made, but the beds are almost vertical here and the scree material is all derived from the lowest few metres of the sequence.

Jebel Buhays, section 3. Northeastern corner of Jebel Buhays, just southeast of a television mast, 4 km north of Al Madam, United Arab Emirates. Dhayd Sheet 1:100,000, NG–40–107; grid ref. 788,670.

5. Jebel Thanais (Fig. 4A). Northeastern side of the jebel, about 4 km north of Al Madam, United Arab Emirates. Dhayd Sheet 1:100,000, NG–40–107; grid ref. 783,699.

6. Jebel Aqabah (Fig. 4A). Southwestern face of jebel, forming a steep cliff about 200 m northeast of the tip of Jebel Thanais and about 4 km north of Al Madam, United Arab Emirates. Dhayd Sheet 1:100,000, NG–40–107; grid ref. 785,698.

7. Jebel Faiyah (Figs 2, 4A). One section was logged in detail. A further three were explored but found to be unprofitable: collections were made from only one.

Jebel Faiyah, section 1. Eastern scarp face from the southern nose of the jebel northwards for 500 m, 5.5 km north of Al Madam, United Arab Emirates. Detailed logs were made at the northern end of the section (section 1a) and approxi-

mately midway along (section 1b). Dhayd Sheet 1:100,000, NG–40–107; grid ref. 800,697 to 802,702.

Jebel Faiyah, section 2. Eastern scarp face of the jebel approximately 3 km NNE of the southern tip of the jebel, and 8 km N of Al Madam, United Arab Emirates. Dhayd Sheet 1:100,000, NG–40–107; grid. ref. 806,722. All but the lowest 2 metres of outcrop was highly indurated and thus fossils collected come from only these basal beds.

8. Qarn Murrah (Fig. 4A). Northeastern slope of the qarn, some 8 km west of the northern tip of Jebel Faiyah and 15 km north of Al Madam, United Arab Emirates. Dhayd Sheet 1:100,000, NG–40–107; grid ref. (approx.) 760,795. The section here was small and the rocks hard and well-lithified, making collecting difficult. No section was logged.

LITHOFACIES AND FAUNAL ASSEMBLAGES

A total of 14 sections were logged and their macrofauna recorded. Lithological samples were collected systematically from the thickest sequence, (Jebel Rawdah, section 2), and sectioned for petrographic analysis. The lithological descriptions given for other sections are based solely on field observations and are consequently of a preliminary nature. The results of this work are summarized in the measured sections (Figs 5–11) and in the faunal lists of the Appendix. As the successions in the various jebels differ significantly and correlation between jebels was not initially obvious, each succession is documented in turn before attempting a synthesis.

Jebel Rawdah (Figs 5–7)

1. Sedimentary lithofacies at section 2. From field logging and petrographic analysis we recognize the following major lithofacies:

Facies 1. The succession commences with an ultrabasic clast conglomerate (bed 1). This can reach more than 10 m in thickness in places, and comprises well-rounded clasts of mean size 10–20 cm. There are rare rounded fragments of rudist and occasional acteonellid gastropod shells. Similar sediments in the region have been interpreted as beach deposits by Skelton *et al.* (1990), a view supported in our interpretation.

Facies 2. There then follows a mixed clastic-bioclastic coarse sand, with relatively well-rounded coarse sand to gravel-sized clasts, ca. 1 m thick (beds 2–4). This includes up to 20% ultrabasic sand. The high sphericity and excellent sorting of the clasts indicates these sediments accumulated in a very high-energy environment; either intertidal or very shallow subtidal. We interpret these as shoreface sands.

Facies 3/4. The majority of lower beds in the succession are poorly sorted mollusc-coral-foraminiferal packstones that contain components of three size classes: (i) clay and silt-grade carbonate, now replaced by a weak ferroan calcite microsparite cement; (ii) well-rounded, fine sand-grade particles, with a sizeable component of ultrabasic grains in the lower beds, as well as rolled and bored mollusc and echinoderm debris; (iii) diverse larger bioclasts which vary in composition from bed to bed. There are two broad facies distinguishable in hand specimen on the basis of the major clast component.

Facies 3 is a poorly sorted calcarenite rich in mollusc clasts (especially rudist clasts) as well as obvious ultramafic sand-

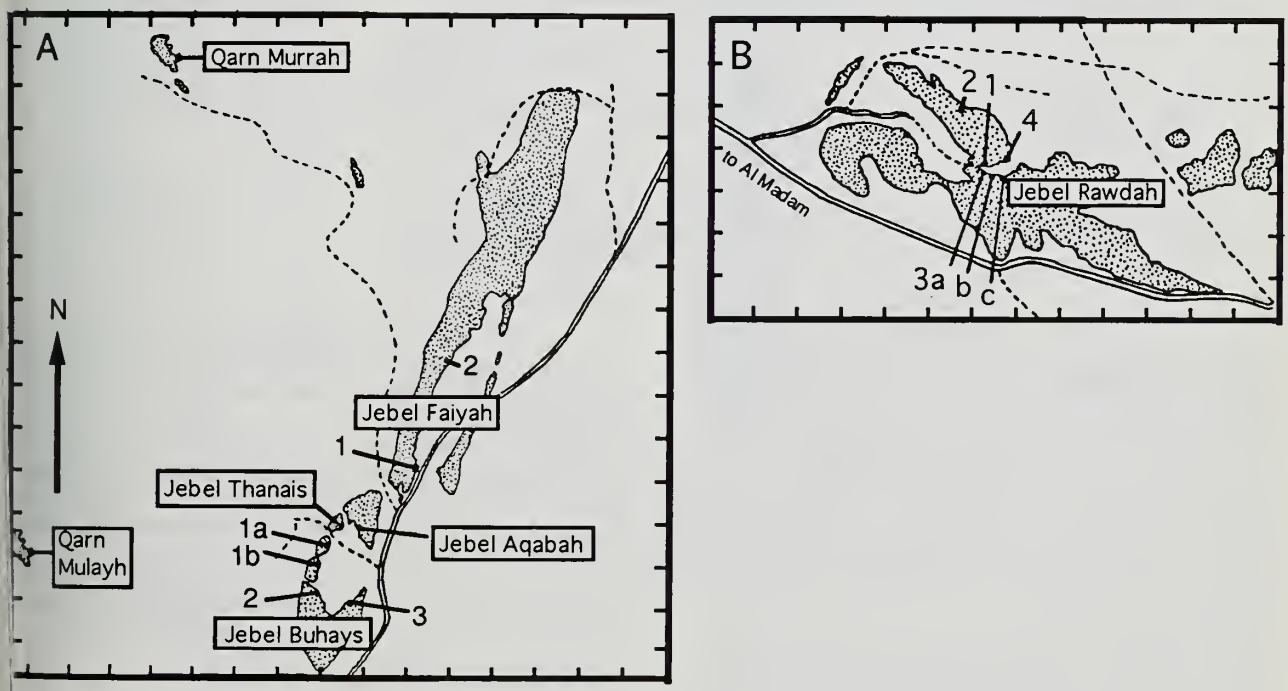
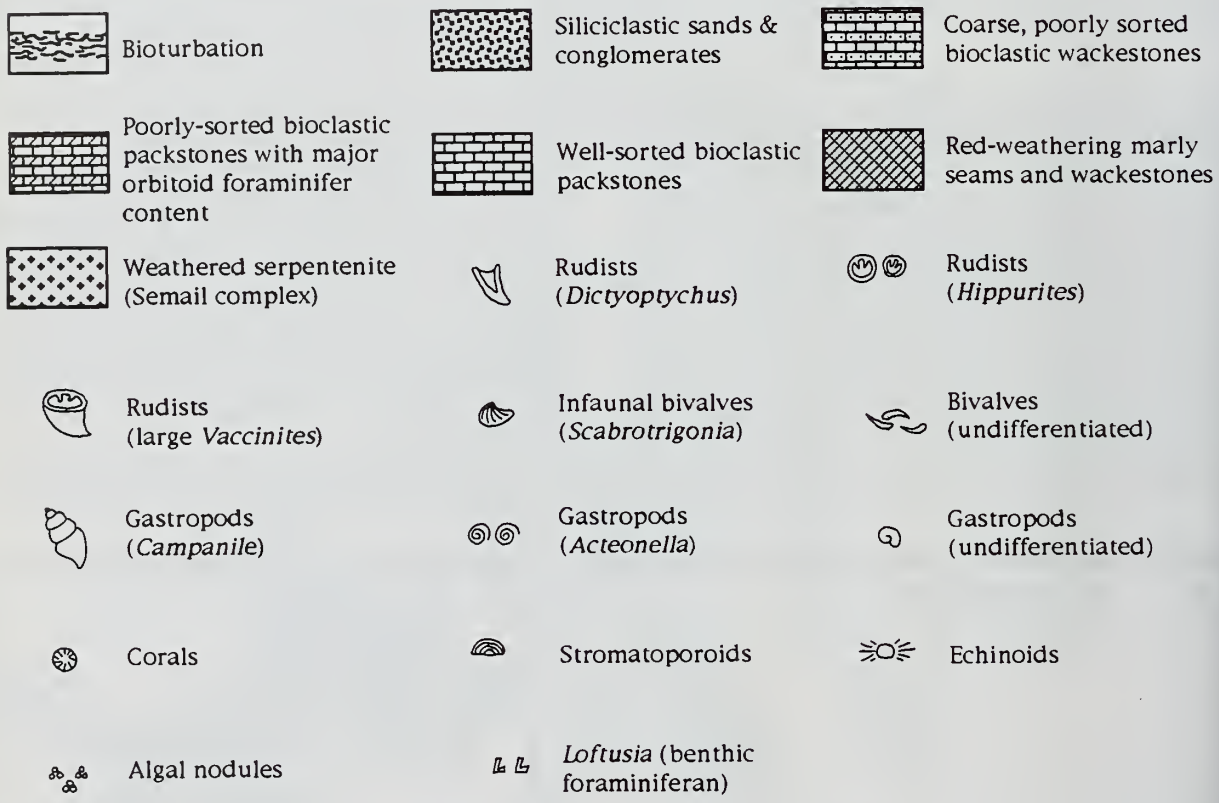


Fig. 4 Detailed locality map for Qarn Murrah and Jebels Buhays, Thanais, Aqabah and Faiyah (map A), and Jebel Rawdah (map B). 1, 2, 3, 4 = studied sections. For regional placement see Fig. 2.

Figures 5 - 11. Measured sections through the late Cretaceous Qalah and Simsima Formations. Locality details for each named section are given in Figures 2 - 4 and in the text. Logs are drawn to a scale of 5 mm = 1 m for Figs 5, 6, 9 - 11 and 4 mm = 1 m for Figs 7 and 8. Lithological data are based on field observations except for Jebel Rawdah, section 2. Faunal assemblages noted in the right-hand column are also largely based on field observations; full faunal lists for each section are given in Appendix 1.

Symbols used are as follows:-



grade clasts. This makes up the lower beds (beds 5–10) and includes various thin coquina lenses and horizons of coarse coral and rudist debris.

Facies 4 is characterized by an abundance of orbitoid foraminiferan clasts, with fragments of the rudist *Dictyoptychus* common in lower beds (beds 11–12) and of corals in upper beds (beds 15–19). Furthermore, in these higher beds there are also layered blebs of mud-grade carbonate, incorporating sand-grade bioclasts, which are storm-reworked pellets of mud-grade sediment.

Skelton *et al.* (1990) interpreted facies 3 and 4 as deposits formed in a point bar and tidal channel system. However, the original presence of significant quantities of mud-grade carbonate (probably algal aragonite) in this facies, together with its overall poor sorting is taken as evidence of deposition below normal wave-base. The sand-grade component, which is well-rounded and was originally well-sorted, was probably washed in from shallower water (intertidal to shallow subtidal) by storm activity.

Metre- to several metre-scale bedding cycles (most obviously expressed in banded rhodolite development) are apparent in this facies. The origin of such cyclicity is enigmatic, but the deeper-water setting proposed above militates against their being tidal channel in origin.

Facies 5. The upper part of the succession (comprising beds 19–28) is composed of well-sorted, well-rounded sand-grade bioclasts, grain supported and originally containing little or no calcite mud. There are rare larger (up to 1 cm) bioclasts. The foraminiferal component is dominant (50–60%) and includes both broken and rolled orbitoids, entire small rotalines and miliolines. Up to 10% dasycladacean algae also occurs. This facies was deposited significantly above wave-

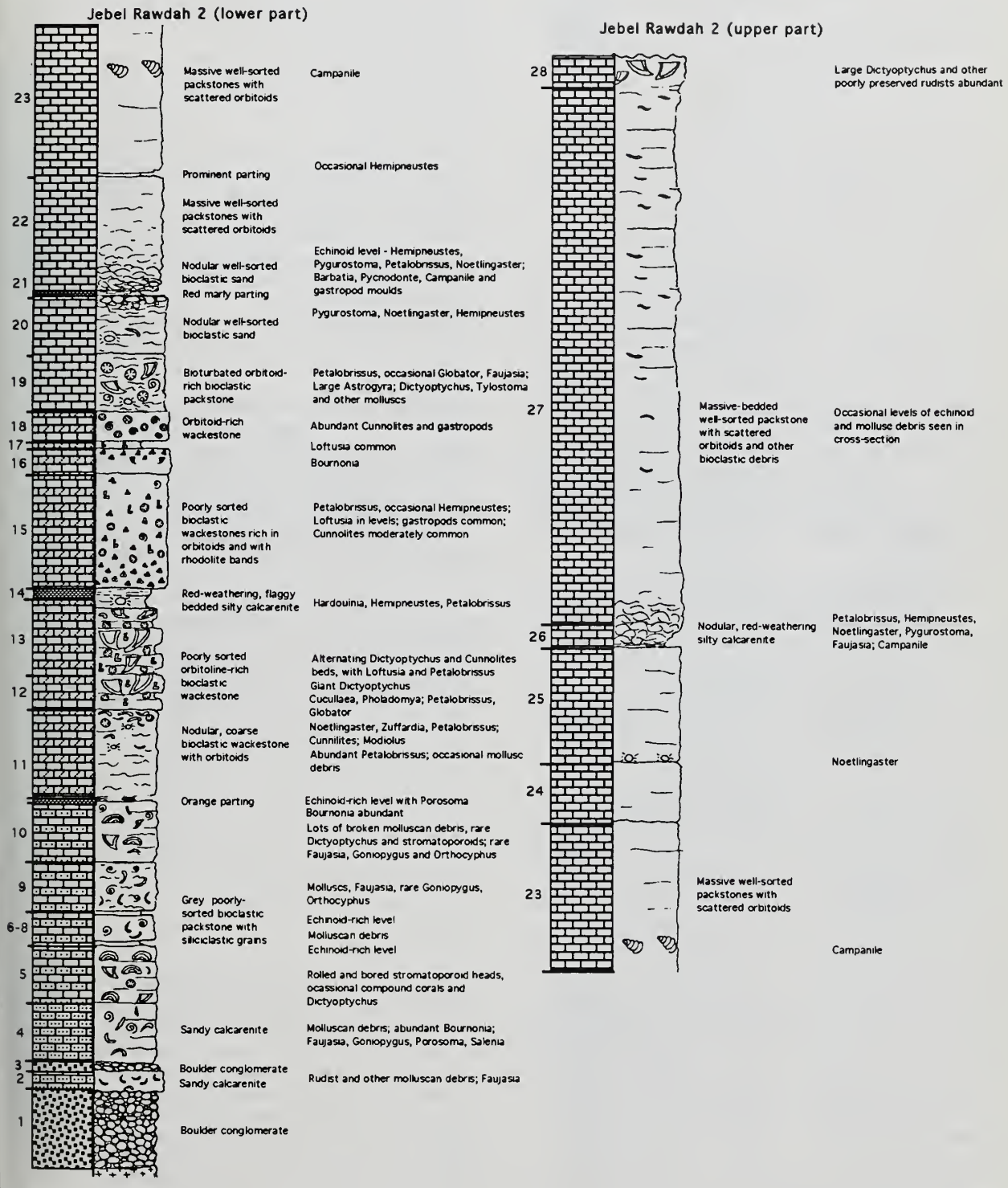


Fig. 5 Measured section made at Jebel Rawdah, section 2 (see Fig. 4B for locality).

base in a high energy environment, as indicated by the high degree of sorting and lack of mud-grade carbonate.

2. Succession and faunal assemblages (Figs 5–7). Lateral variation is considerably greater here than at any other jebel. Of particular note is the marked attenuation of the entire lower part of the succession eastwards along Jebel Rawdah 3 (Fig. 7). However, although there is marked variation in bed development from one section to the next, the same general succession can be identified at them all.

The basal pebble to boulder conglomerate varies tremendously in thickness, being best developed at Jebel Rawdah 3a and thinnest at Jebel Rawdah 4. There is very little in the way of sand and grit lenses developed, the entire sequence being exceedingly coarse. However, rare *Acteonella* are present in the upper part of the sequence at Jebel Rawdah 3.

The coarse siliciclastics are succeeded by a thin transitional sandy calcarenite facies quickly followed by grey, shelly bioclastic limestones with obvious scattered sand-sized grains of ophiolite. These basal calcarenites are relatively coarse and are well-lithified. At several horizons the beds contain rolled and often bored heads of the compound coral *Actinacis*, some up to 30 cm in diameter, as well as a variety of allochthonous compound corals and mollusc debris. The infaunal cassiduloid *Faujasia eccentripora* is the only obvious autochthonous element in these beds. The basal bed at Jebel Rawdah 4 is notable for the abundance of transported hippuritid and *Durania* rudists. Within the succession at section 2 there are two closely-spaced shell-rich partings with many echinoids, notably *Goniopygus*, *Phymotaxis* and *Orthocyphus*.

Towards the top of this calcarenitic succession is a prominent, orange-weathering, silt-enriched parting (top of bed 10, section 2). This bed is thickest at Jebel Rawdah 2 and has the same echinoid fauna as found below. The overlying beds are still bioclastic calcareous sands but are more poorly sorted, and in places include significant amounts of sand-grade siliciclastics (e.g. section 1, bed 1). They contain the solitary discoidal coral *Cunnolites* and the infaunal bivalves *Cucullaea*, *Pholadomya* and, in places, *Scabrotrigonia*. Orbitoid Foraminifera occur but only in minor abundance.

Overlying these poorly sorted bioclastic limestones come orbitoid-rich packstones, with abundant specimens of the infaunal cassiduloid echinoid *Petalobrissus*. At the base there is a distinctive infaunal echinoid assemblage dominated by the cassiduloid *Zuffardia* and the epifaunal regular echinoid *Noetlingaster*. One to three metres above the base of orbitoid-rich limestones there is a prominent horizon of very large examples of the rudist *Dictyoptychus*, probably in life position. The succeeding 2–3 metres at Jebel Rawdah 2 consist of beds with *Dictyoptychus* alternating with beds rich in the solitary discoidal coral *Cunnolites*, the larger benthic foraminifer *Loftusia*, and the infaunal cassiduloid echinoid *Petalobrissus*. It is at about this level that the ammonite *Brahmaites (Anabrahmaites) vishnu* (Forbes, 1846) was found at Jebel Rawdah 1. A second major silt-enriched level occurs above this, and these flaggy beds yield a fauna of large infaunal cassiduloid and holasteroid echinoids (*Hardouinia*, *Hemipneustes*).

There then follows a succession of rather fine, muddy, thoroughly bioturbated, bioclastic limestones with orbitoid Foraminifera and bands of rhodolite nodules. There are occasional infaunal holasteroid echinoids (*Hemipneustes*), but the predominant component of the fauna are the solitary discoidal corals (*Cunnolites* and *Asteraea*) and a variety of gastropods, together with the larger benthic foraminifer *Loftusia*.

The succeeding bed (bed 19, section 2) contains large compound corals (*Astrogyra*) and rudist material. This bioclastic limestone also has occasional large infaunal echinoids and a mixture of other molluscs.

The next few metres are composed of well-sorted, red-weathering, silt-rich calcarenites. They have a significant fine siliciclastic content, particularly in the *Hemipneustes* beds (bed 21, section 2).

There then follows a thick and fairly monotonous sequence of well-sorted calcarenites with sparse to moderate numbers of orbitoid Foraminifera. This facies has little in the way of macrobenthos, other than the occasional *Dictyoptychus*, *Noetlingaster* or *Campanile*. There is, however, one distinct nodular, red-weathering, silt-enriched calcarenite level which has a diverse fauna of infaunal cassiduloid and holasteroid echinoids towards the top.

Large, poorly preserved rudists occur in abundance at the top of the sequence and the succession is terminated by an unconformity.

3. Palaeoenvironmental interpretation. It is clear that at Jebel Rawdah local sedimentation patterns were controlled by topographic variation of the underlying sea-floor. In particular, the south-eastern corner appears to have been relatively starved of sediment compared, for example, to the northern flank of the jebel.

In environmental terms deposition commenced with pebble conglomerates laid down in a near-shore high-energy environment around the newly emergent obduction complex. These were replaced rapidly, as the obduction complex subsided and the region became flooded, by coarse, poorly sorted carbonate sands. These contain significant amounts of reefal debris and represent immediately offshore sands accumulating below wave-base. The following sequence of mixed orbitoid-rich platform shoals alternating with more protected platform bioclastic sands with their gastropod and solitary coral fauna probably represent local variation between topological highs and dips over a broad carbonate platform in probably no more than 10–20 m water depth. Towards the top of the section a regressive phase is marked by a brief period of patch-reef development and the influx of fine siliciclastics. The remainder of the succession is composed of shallow-water calcarenites formed within active wave-base and supporting only a sparse fauna.

Jebel Huwayyah.

1. Lithological succession and faunal assemblage (Fig. 8). The general succession is similar throughout the jebel, though with some lateral variation in bed thicknesses. The lowest beds, best seen at section 1, consist of poorly sorted silts and sands with rare lenses of the oyster *Acutostrea*. The succession passes up into pebble- and grit-sized conglomerates and cross-bedded siliciclastic sandstones, the pebbles being predominantly igneous in origin and well-rounded. Bed 7 is of particular interest because it contains broken fragments of thick-shelled rudists, and occasional pebbles that are encrusted by *Acutostrea* or, more rarely, by small compound corals.

After a small gap in exposure there follows a succession of highly bioturbated, poorly sorted, brown-weathering, silt-rich

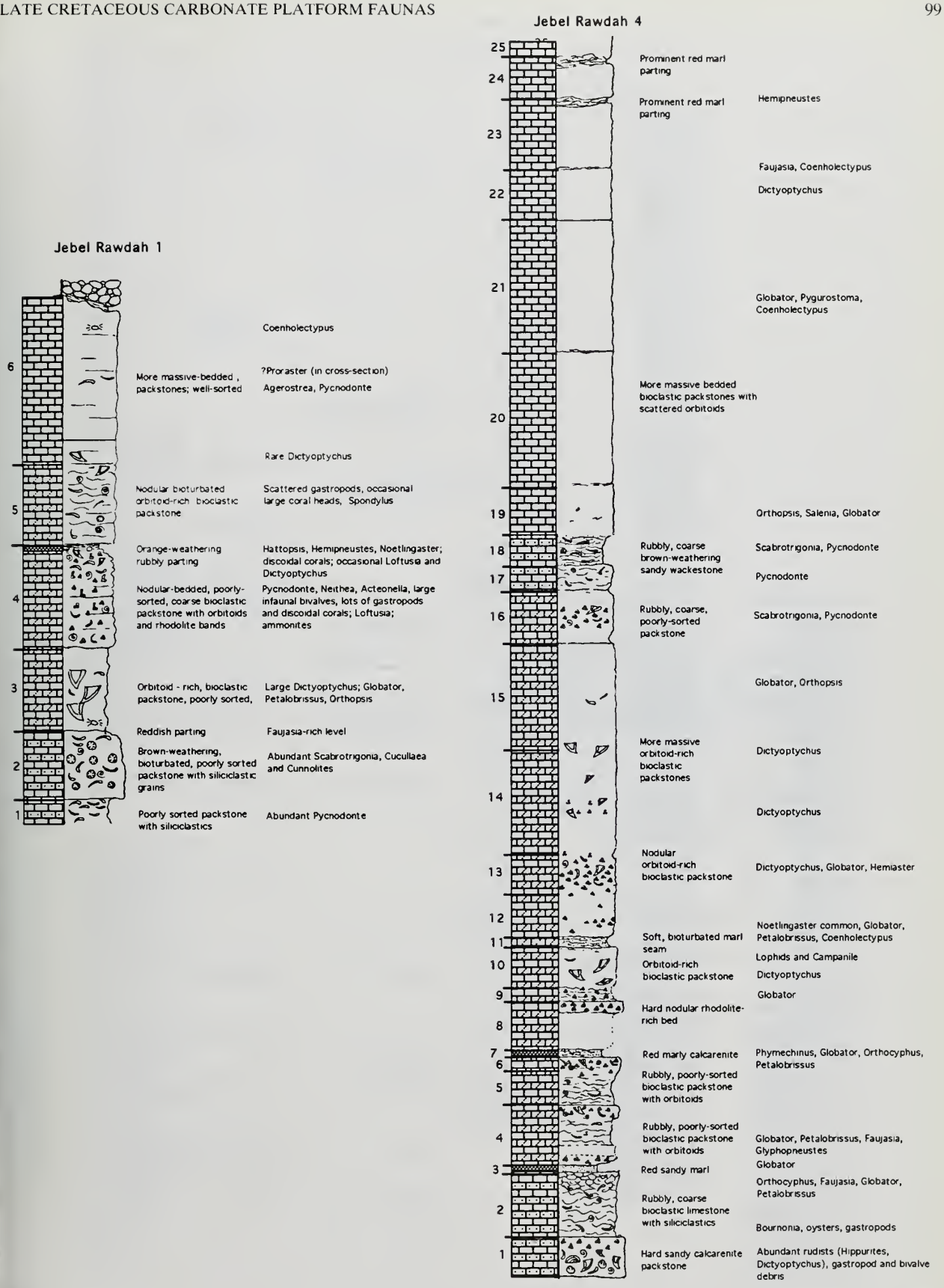


Fig. 6 Measured sections made at Jebel Rawdah, sections 1 and 4 (see Fig. 4B for locality).

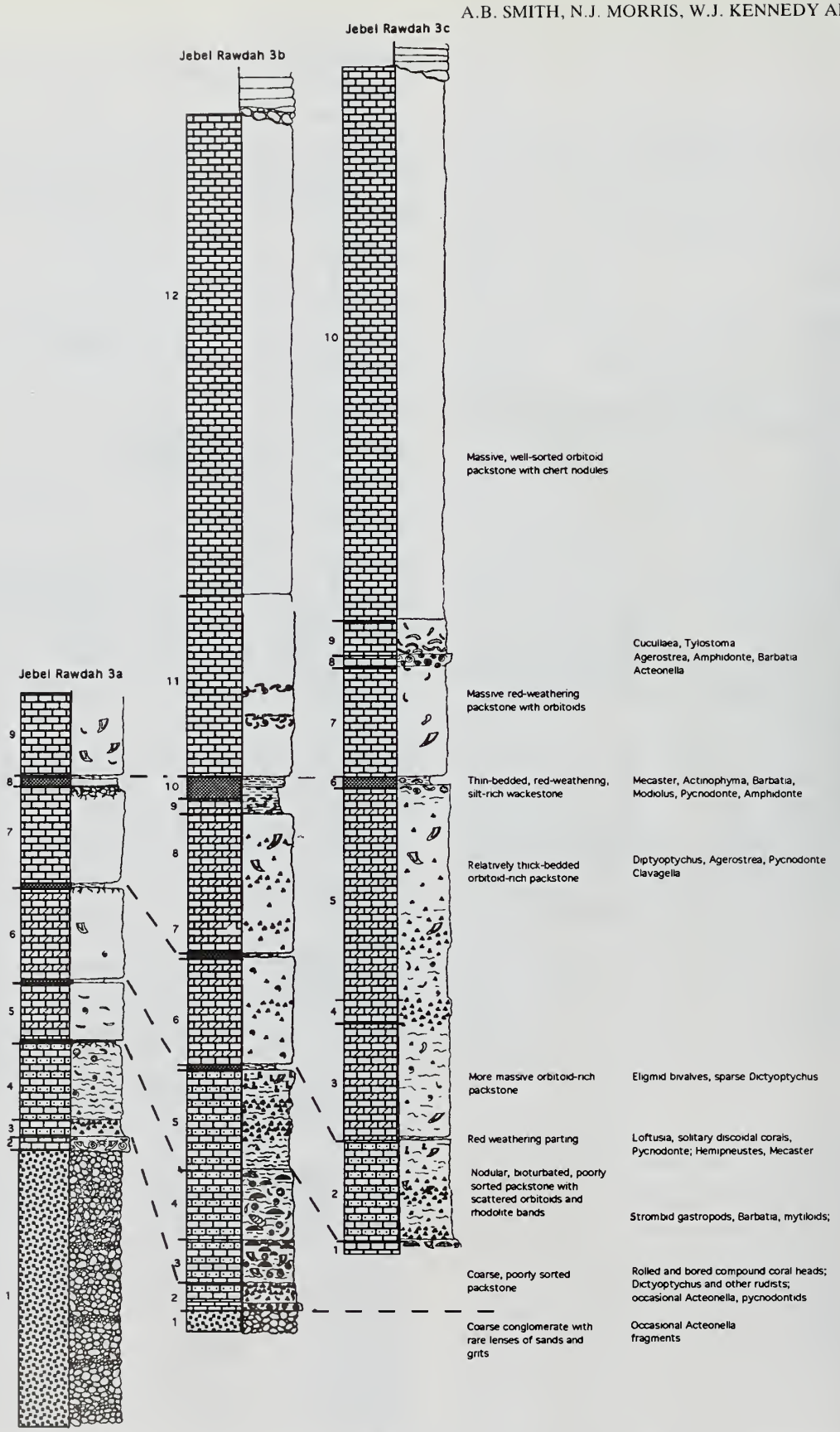
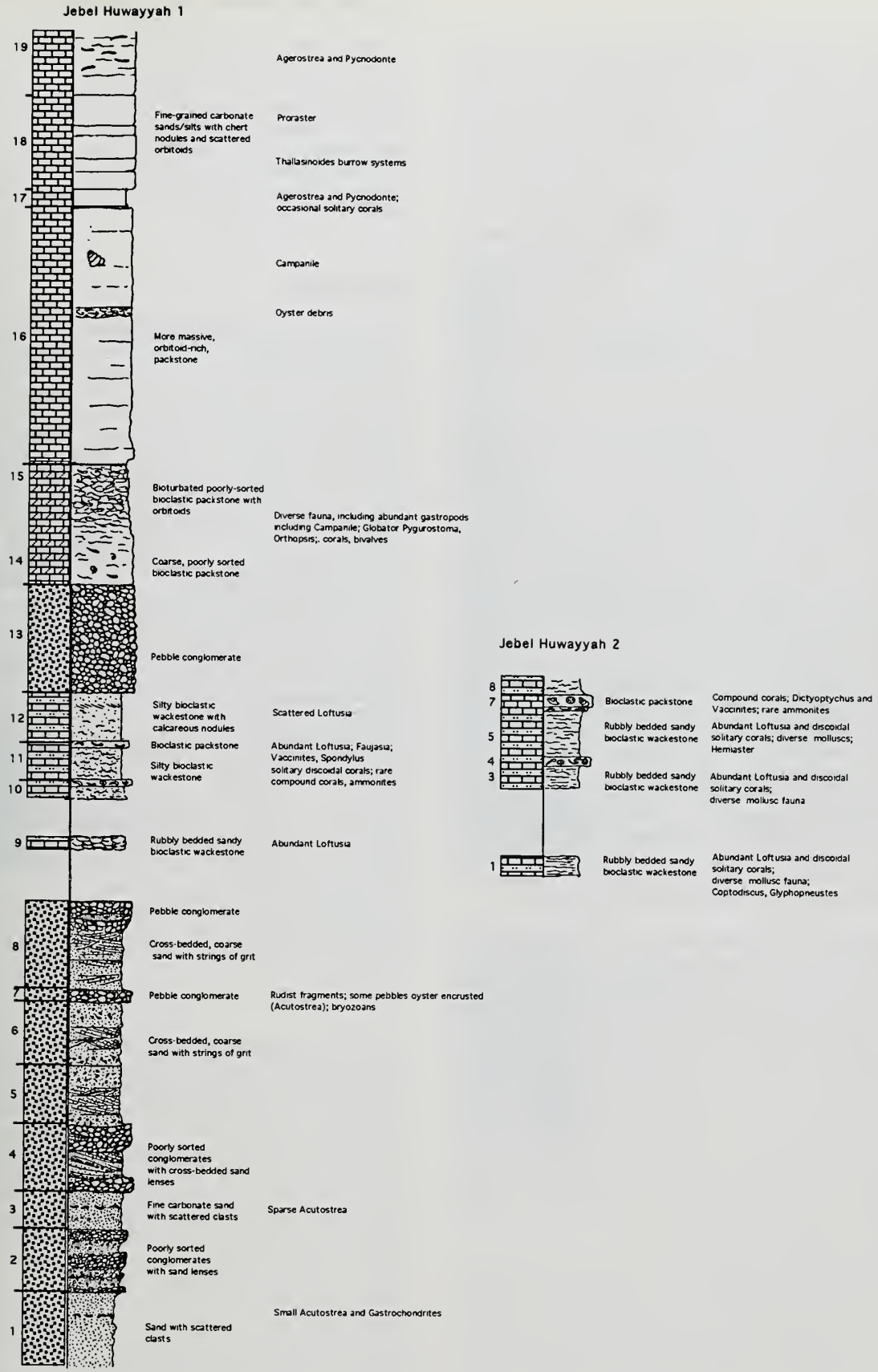


Fig. 7 Measured sections made at Jebel Rawdah, section 3 (see Fig. 4B for locality).



ig. 8 Measured sections made at Jebel Huwayyah, sections 1 and 2 (see Fig. 3 for locality).

bioclastic limestones with significant amounts of dark-green, sand-sized, igneous grains. These beds contain abundant specimens of the benthic foraminifer *Loftusia* as well as scattered molluscan debris and occasional infaunal spatangoid echinoids. The large solitary button coral *Cunnolites* is also abundant. Within this facies are two prominent marker limestones that are thicker and better developed on the western limb of the jebel. They contain a rich fauna of compound corals, the hippuritid rudist *Vaccanites* and the occasional large, tall-spired gastropod *Campanile*. None of the rudists are found in life position and the beds appear to represent allochthonous accumulations. However, the base of the upper of these beds is typically rich in *Spondylus* and *Plicatula* that are clearly not transported, as most are preserved with both valves connected. Ammonites, some quite large, are occasionally found at this level, presumably transported into this environment.

Above the *Loftusia*-rich beds comes a sequence of less fossiliferous silty bioclastic carbonate sands, which are in turn succeeded by a thick pebble conglomerate. This conglomerate is composed of very well-rounded clasts, and represents such an anomalous lithofacies change that it must have formed through exposure and reworking of earlier conglomeratic beds. Above the conglomerate siliciclastics abruptly disappear and are replaced by relatively clean bioclastic limestones of the Simsima Formation. This starts with an initial shell-rich bioclastic limestone, followed by 2 to 3 metres of highly bioturbated and poorly sorted bioclastic limestones with sparse sand-grade siliciclastics. These sediments are very fossiliferous, the fauna dominated by shallow infaunal cassiduloids and holectypoids (*Pygurostoma* and *Globator*), infaunal naticids and other gastropods, including *Campanile*. Occasional pectinid bivalves are also present.

Higher beds pass into less fossiliferous and much more massive and well-sorted, orbitoid-rich carbonate sands and silts. There is at least one level of thallasinoid burrows. Rare *Dictyoptychus* are found here. The orbitoid content of the sediments decreases upwards so that higher beds, which contain the epifaunal bivalves *Agerostrea*, *Pycnodonte* and the infaunal spatangoid *Proraster*, are finer-grained carbonate sands or silts with relatively few orbitoid clasts.

2. Palaeoenvironmental interpretation. The succession commences with unconsolidated subtidal sand and cobble beds deposited around the margins of the newly emergent obduction complex. The sequence shallows upwards into the shoreface facies of bed 7, with increasing cross-bedding and coarser clastic content. The clastic supply then sharply diminishes, presumably marking the final flooding of nearby ophiolite islands, and the initiation of carbonate platform development. The poorly sorted *Loftusia*-rich muddy carbonate sands represent extremely shallow-water, back bar or lagoonal deposits formed in a protected environment below wave-base. Coral-hippuritid thickets were able to develop locally and occasional open-water ammonites were washed in. The thin, well-sorted calcarenitic sands with *Faujasia* may represent protected beach-face sands.

A brief regression caused by local uplift led to the exposure of Qahlah Formation conglomerates, or their source rock, and pebble conglomerates were once more briefly deposited in a high-energy shallow marine environment (bed 13). This was short-lived and carbonate platform conditions returned once again, bringing about the more or less complete elimination of siliciclastic components. This presumably marks a renewed phase of subsidence with transgressive seas once more flooding the region and cutting off siliciclastic input. The initial coarse bioclastic fossiliferous sands (bed 14), we interpret as deposits formed at or immediately below normal wave-base. They are replaced immediately upwards by thick beds of shallower-water orbitoid-rich carbonate sands with little macrobenthos, formed within wave-base. These are succeeded in turn by fine carbonate sands and silts suggestive of shelf-basinal conditions.

Jebel Bu Milh

1. Lithological succession and faunal assemblages (Fig. 9). The succession begins, as in Jebel Huwayyah and elsewhere, with a rather thick series of well-rounded pebble conglomerates, grits and coarse clastic sands, with some small-scale cross-bedding. Although largely unfossiliferous, occasional clumps of the rudist *Durania* can be found, apparently *in situ*. Towards the top is a 1–2 m thick conglomeratic sequence, packed with well-sorted shells of the gastropod *Acteonella*, showing good current alignment of individual layers. Occasional specimens of the rudist *Pseudosabinia* also occur. The succeeding clastic sands are strongly cross-bedded and contain occasional *Acteonella* specimens, as well as large logs bored by lithophagid bivalves.

There is then a sharp reduction in the siliciclastic content of the sediments and the succeeding 1.0–1.5 metres are composed of highly fossiliferous calcarenitic limestones with sparse sand-sized quartz grains. The basal bed is a fine, silty calcarenite that is highly nodular and extensively bioturbated. It contains rare nautiloids and ammonites and a rich gastropod fauna, with naticids and neogastropods dominating. An erect, branching sponge is a common element of this fauna, though none appear to be preserved *in situ*. Above this basal carbonate bed is a thin, red-weathering, silt-enriched parting, followed by a harder, less bioturbated shelly bioclastic limestone that contains at its base the large tall-spired gastropod *Campanile* in some abundance, together with *Acteonella*, *Dictyoptychus* and other large molluscs.

Succeeding beds are well-sorted orbitoid-rich bioclastic limestones. These contain little in the way of macrofauna except for a very distinctive horizon of large hippuritid rudists *in situ*, some 4–5 m above the base of the limestone succession.

2. Palaeoenvironmental interpretation. The succession at Jebel Bu Milh commences with quartz sands, gravels and conglomerates representing open-water, nearshore deposits around the newly emergent obduction complex. The succession shallows upwards, with the *Acteonella* conglomerates representing open shore-face, shell-lag accumulations at wave base, and the overlying cross-bedded sands with beached driftwood representing tidal sandbars. The clastic succession is abruptly replaced by carbonate platform deposits, presumably as nearby islands became submerged. A thin deposit of silty bioclastic limestone rich in naticid gastropods represents shallow subtidal sands, possibly formed at wave base in a protected back-bar environment. The presence of the large neritid *Lisocheilus* indicates that shallow rocky substrates lay in the vicinity. The remaining carbonate succession, by comparison with beds at Jebel Rawdah, represent shallow subtidal carbonate sand flats formed above wave base.

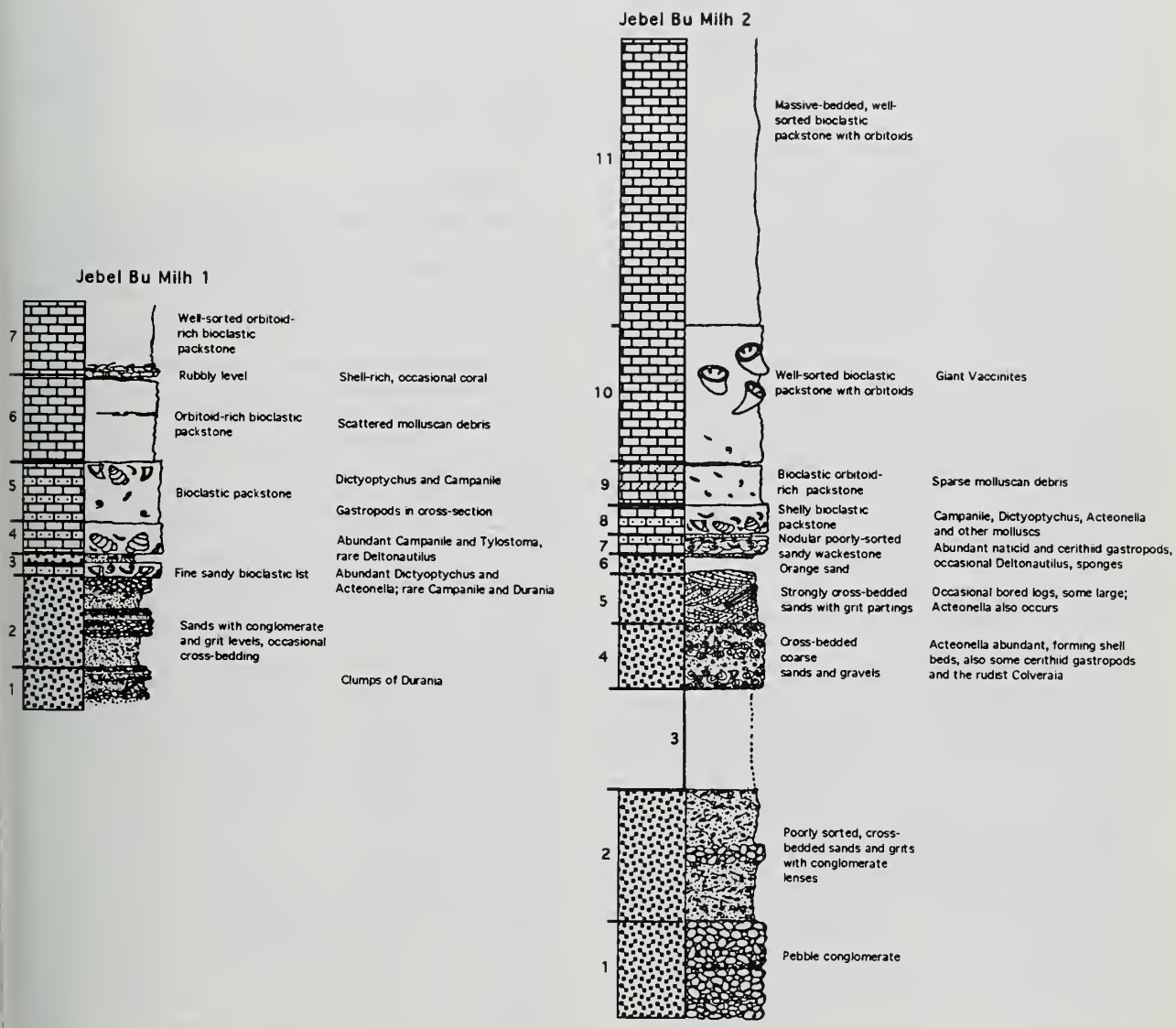


Fig. 9 Measured sections made at Jebel Bu Milh, sections 1 and 2 (see Fig. 3 for locality).

Jebels Buhays, Thanais and Aqabah

1. Lithological succession and faunal assemblages (Fig. 10). These three jebels show virtually the same succession and can therefore be treated together. The initial siliciclastic succession of pebble conglomerates, sands and gravels is thinner than at Jebel Rawdah or Jebel Bu Milh. At Jebel Aqabah the succession commences with a 50 cm well-sorted calcarenite resting directly on top of slightly weathered ophiolite. This basal bed is notable for the small, uniform size of its fossils; a small heteromorph ammonite, *Glyptoxoceras* sp., was recovered from here. Elsewhere the basal contact is not seen. Towards the top of the clastic sequence, at Jebel Buhays, section 1, come 3 to 4 metres of laminar and cross-bedded sands. These contain a fauna of infaunal venerid bivalves and small turreted gastropods.

As elsewhere, there is a sudden elimination of siliciclastics coincident with the onset of biocalcarenite deposition, marking the base of the Simsima Formation. The limestone succession begins with a hard, 80 cm thick, sandy bioclastic shell bed full of the gastropods *Acteonella* and *Campanile*, the echinoid *Goniopygus* and rudist fragments (*Durania* and hippuritid), as well as other molluscan debris. Occasional compound corals occur at this level, but apparently not *in situ*.

The succeeding 3 to 4 metres consist of highly bioturbated, poorly sorted coarse- to medium-grained bioclastic limestones, with scattered orbitoid foraminifera that increase in abundance upwards. These beds are rich in infaunal echinoids (cassiduloids, especially *Pygurostoma*, and the holectypoid *Globator*) as well as small epifaunal regular echinoids. They are also rich in gastropods and bivalves, both infaunal and soft-bottom epifaunal forms. The only rudist to occur here in abundance is the small recumbent *Glabrobournonia*. Within this succession there is a major red-stained, silt-enriched layer that immediately overlies a thin bed of fine, ?dolomitized limestone.

There is then a second major shell-lag deposit, full of large sponge-bored shells of *Acteonella* and other molluscs. Above this the bedding becomes much more massive and the limestones better sorted and cemented. Immediately overlying the *Acteonella* shell bed is an orbitoid-rich packstone with rhodolite bands and a low diversity fauna of the rudist *Dictyoptychus* and the gastropod *Campanile*.

A major red-weathering silt-enriched horizon occurs towards the top of the sequence and is immediately overlain by a one metre thick brown-weathering silty limestone, rich in tall cylindriform hippuritids. Associated here is the echinoid *Codiopsis*, indicative of rocky shore habitats. The silt-enriched bed records a marked increase in the clastic component at this level. It is overlain by massive-bedded, well-sorted carbonate sands/silts with orbitoids.

2. Palaeoenvironmental interpretation. The palaeoenvironmental setting is similar to that seen elsewhere, with shallow marine sands, gravels and conglomerates deposited above active wave base. The basal calcarenite at Jebel Aqabah probably represents a shoreface sand, as suggested by the well-sorted clasts and fossils.

These sands, gravels and conglomerates are replaced abruptly by coarse, poorly sorted bioclastic calcarenites containing a diverse molluscan and echinoid fauna. These beds are highly bioturbated and were deposited in a protected environment below wave-base, possibly in a shallow lagoonal setting. The occasional large compound coral near the base suggests that reefal patches developed nearby. Periodic minor adjustments in sea-level resulted in red-weathering, silt-enriched partings and beds, marking temporary influxes of fine iron-rich silt-grade clasts while thin dolomitic levels may signify temporary supratidal exposure.

A subsequent regressive phase led to the deposition at wave base of the *Acteonella* shell-lag of bed 11 followed by orbitoid-rich carbonate sands with a low diversity macrofauna. We interpret these well-sorted and well-lithified beds as shallow water platform shoals formed above active wave base. There was a brief event that created the upper iron-rich siltstone band (bed 14) which was followed by a bed with hippurited thickets and the shallow-water echinoid *Codiopsis*, indicative of nearshore conditions. Shallow-water carbonate shoals form the remainder of the succession.

Jebel Faiyah

1. Lithological succession and faunal assemblages (Fig. 11). Here the sequence overlying weathered ophiolite begins with pebble conglomerates, with interspersed grit and sand lenses becoming more common towards the top. Occasional fragments of thick-shelled mollusc are present indicating a marine origin for the unit.

As in other sections, there is an abrupt change to carbonate sedimentation, commencing with a 40–50 cm shell bed full of *Acteonella*, together with lesser amounts of rudist fragments and other thick-shelled molluscan material. The succeeding 3 metres consist of highly bioturbated, poorly-sorted bioclastic limestones, with rhodolites and orbitoid foraminifera, a diverse fauna of gastropods, small regular echinoids and *Dictyoptychus* bands.

There is a major, 10 cm thick, red-coloured, silt-enriched bed which, as at Jebel Buhays, is interpreted as marking a minor change in sea-level with increased erosion of lateritic soils from the hinterland. It is succeeded by *in situ* coral thickets with associated hippuritid rudists (bed 6, section 1a). The majority of *in situ* colonies are erect, branching forms some 50 cm in diameter, with intermixed erect colonies of cylindrical hippuritids. A variety of other colonial corals and rudists also occur. There is also a moderately diverse fauna of small regular echinoids, such as *Glyphopneustes*, and small gastropods at this level.

Next come a few metres of thick-bedded, orbitoid-rich bioclastic limestones with occasional levels of *Dictyoptychus* and rhodolites but little else. There is then a return to red-weathering, poorly sorted bioclastic limestones with a significant silt-grade component (beds 8–10). These beds appear to be relatively iron-rich. The fauna is diverse and dominated by the epifaunal bivalves, *Pycnodonte* and *Agerostrea*. Small discoidal corals (*Cunnolites*), occasional compound corals, the foraminifer *Loftusia* and rudist *Glabrobournonia* all occur at this level.

The succeeding thick sequence of rather massive, well-lithified and well-sorted carbonate sands, rich in orbitoid foraminifera, but with no observable macrofauna, is truncated by an erosion surface.

2. Palaeoenvironmental interpretation. The succession begins with shallow-water sands and gravels deposited above active wave base. In places they may even become intertidal or supratidal (Skelton *et al.* (1990) reported the presence of sedimentary structures indicative of intertidal or supratidal

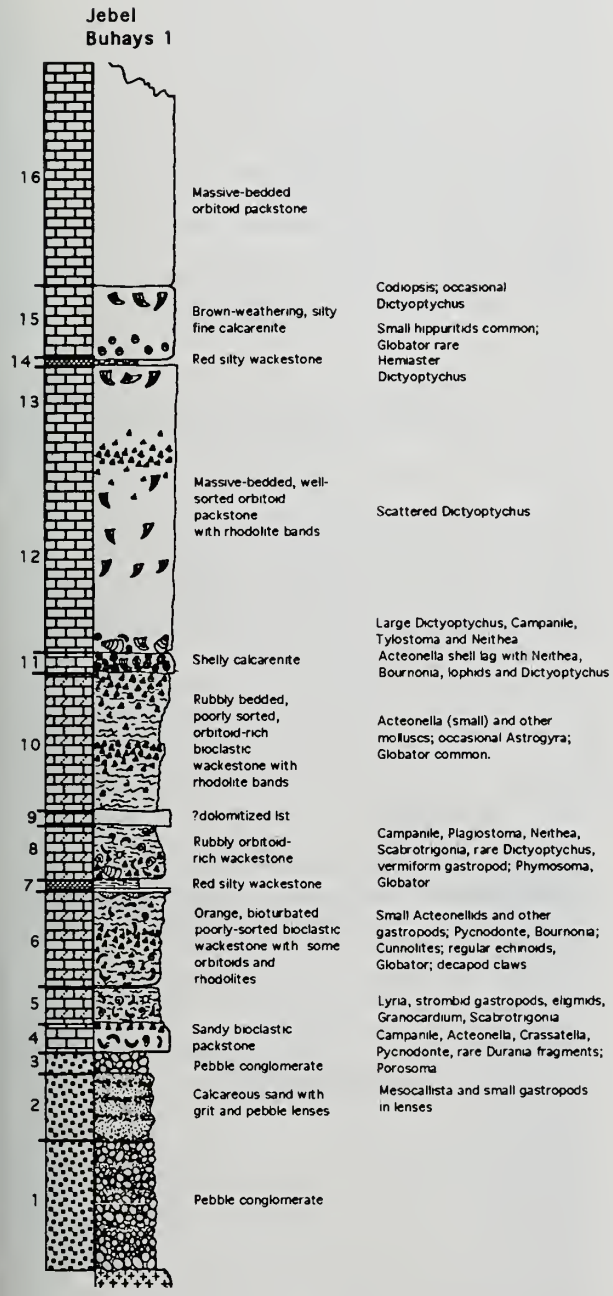


Fig. 10 Measured sections made at Jebel Buhays, sections 1 and Jebel Aqabah (see Fig. 4A for locality).

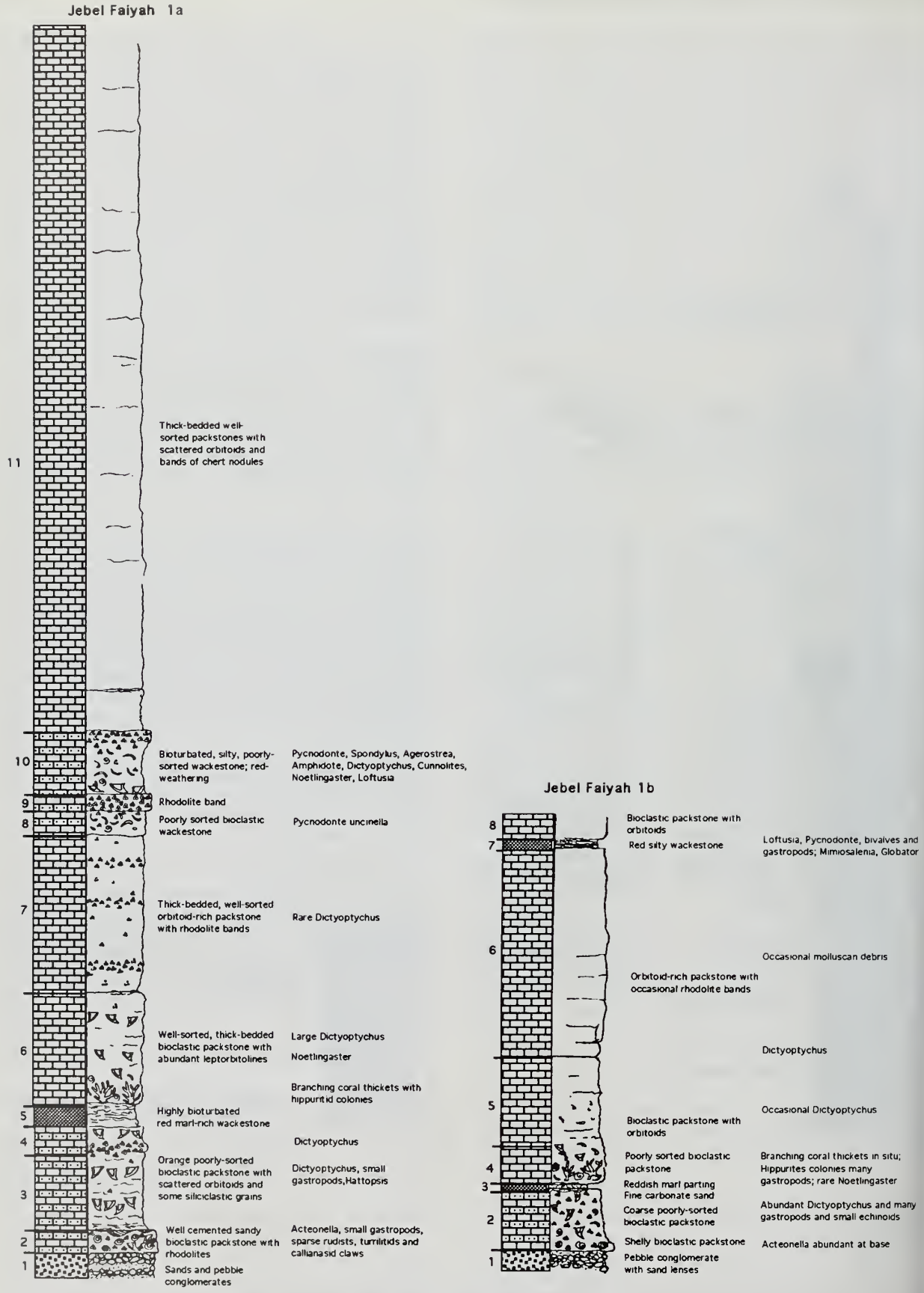


Fig. 11 Measured sections made at Jebel Faiyah, sections 1a and 1b (see Fig. 4A for locality).

environments from these beds). Clastic input ceased suddenly, marking a major transgressive event, and was replaced by carbonate deposition. The carbonate succession began with a transgressive shell-lag deposit rich in acteonellids, after which shallow lagoonal conditions were established for a short period. There was then a minor shift in sea-level, creating a silt-enriched band, which was immediately followed by the establishment of coral-rudist level bottom reefal thickets and peri-reefal bioclastic sands. These in turn were quickly replaced by shallower-water bioclastic carbonate sands with abundant orbitoid foraminifera. These we interpret as shallow-water platform shoals formed above active wave base. Later, a second transgressive phase, marked by an input of siliciclastic material, brought a brief return to deeper water conditions, below active wave base, and the establisment of a more diverse fauna once again. This, however, was short-lived and shallow-water shoal conditions quickly returned with the deposition of massive bedded carbonate sands and the virtual disappearance of benthic fauna.

GENERAL PALAEOENVIRONMENTAL SYNTHESIS

The autochthonous late Cretaceous succession was deposited over a deeply weathered surface of ultrabasic rocks, which must have been exposed subaerially for some time. Initial deposits were locally derived conglomerates and grits formed around the shores of the newly uplifted ophiolite massifs. Pebbles and boulders are well-rounded. Although rudist and acteonellid debris does form a component of these beds, they probably represent shell coquinas washed onshore from subtidal sand-flats rather than autochthonous fauna. There is evidence locally for more sheltered shoreface facies with infaunal bivalves, or for more stable cobble-bottom development, with an *in situ* fauna of encrusting oysters and/or corals. In places, as Skelton *et al.* (1990) note, the rudist *Durania* can be found living *in situ* in cross-bedded sands.

A marine transgression largely drowned these ophiolite islands and led to the onset of carbonate deposition. During this transgression, shoreface reefal debris, with mixed hippuritid and radiolitid rudists and massive compound corals, was deposited as a coarse lag at the base of the transgression. The corals are, for the most part, encrusting forms and are accompanied by a shallow intertidal to immediately subtidal regular echinoid fauna composed of species adapted for life on hard substrata within the zone of active wave surge. Acteonellid gastropods are a characteristic feature of such shell-lag deposits. *Faujasia* is the only common infaunal echinoid in this environment and probably lived in nearshore or shore-face clean, well-washed sediments. Slightly more protected sand beds were colonized by non-siphonate infaunal bivalves such as *Scabrotrigonia* and *Cucullaea*.

This facies was succeeded, as sea-level rose, by a thick succession of rather muddy sands formed at or below active wave base. At some levels the large semi-recumbent rudist *Dictyoptychus* is common, together with bands of rhodolites, dense orbitoid foraminiferal aggregates and abundant small infaunal cassiduloid echinoids (*Petalobrissus* and *Zuffardia*). The sea bottom must have been loose and unconsolidated, lying at or just below active wave base. It regularly received storm-washed bioclastic material.

Elsewhere, solitary discoidal corals and the larger benthic foraminifer *Loftusia* occur in profusion together with pycnodont oysters and a moderately diverse gastropod assemblage in what appears to have been a slightly muddier sand. Infaunal echinoids are more or less absent from this facies, though the small epifaunal regular echinoid *Hattopsis* is often locally abundant and may indicate the presence of algal stands. The molluscan fauna is dominated by gastropods (especially the ?algivore *Acteonella borneensis* and the filter-feeding Umboniidae gen. nov.) and the epifaunal '*Pycnodonte*' *uncinella*. We interpret these beds as stable, possibly algal-bound, sands lying below wave-base. Where this facies occurs close to reefal thickets there is a much higher diversity of regular echinoids accompanied by the holectypoid *Globator*.

Unconsolidated calcarenite shoals, deposited above active wave base, form a major part of the upper succession and contain the lowest faunal diversity. The absence of any large-scale cross-bedding suggests these formed as shallow, broad, subtidal expanses of sand. Rotaline and milioline foraminifera are the predominant bioclasts in this facies, along with dasycladacean algae. It is in this environment that the large selective deposit feeding irregular echinoids *Hemipneustes*, *Pygurostoma* and *Stigmatopygus* are found. The only regular echinoid found to inhabit this environment was *Noetlingaster*.

At Jebel Huwayyah, however, the highest beds appear rather finer grained and contain the infaunal spatangoid echinoid *Proraster*. These may be local basinal sediments deposited below wave base, and possibly represent the deepest water sediments present in the sequence.

The palaeoenvironmental reconstruction that emerges from our combined sedimentological and faunal evidence differs somewhat from that given by Skelton *et al.* (1990). They interpreted the lower part of the Simsima Formation as tidal deposits, whereas we believe that this is inconsistent with both the sedimentological and faunal evidence. The petrography of the sediments indicates deposition below wave base. This is supported by the diverse echinoid fauna, which is also at variance with a tidal environment.

The faunal associations that we recognize represent more-or-less contemporary assemblages that replace one another in vertical succession as a result of shifting sedimentological facies. We found very little stratigraphic variation within single lineages, except in species of the echinoids *Hattopsis* and *Hemipneustes*. Consequently, we believe that the differences in the assemblages reflect variations in palaeoenvironmental conditions over the carbonate platform and represent coexisting communities.

BIOSTRATIGRAPHICAL RESULTS

Maastrichtian biostratigraphic zonation. The Qahlah Formation has been regarded as Campanian or early Maastrichtian in age, and the Simsima Formation as Maastrichtian (e.g. Skelton *et al.* 1990). The boundary between Campanian and Maastrichtian stages has been defined on the basis of a range of biostratigraphic criteria, involving belemnites, ammonites, planktonic foraminifera and coccoliths (amongst other groups). However, recent reviews (Burnett *et al.* 1992, Kennedy *et al.* 1992, Hancock *et al.* 1992) have demonstrated

that these various data do not correspond. Indeed, Obradovich (1993) concluded that the interval between the widely adopted planktonic foraminiferal boundary datum (the extinction point of *Globotruncanita calcarata*) and the widely adopted belemnite definition (appearance of *Belemnella lanceolata*) is at least three million years. There is as yet no agreed definition of the boundary, and subdivisions of the stage into Lower/Upper or Lower/Middle/Upper vary widely between authors. Indeed, in the absence of a clear statement of which definitions of stage and substage limits are used, these terms are near meaningless.

Burnett *et al.* (1992) were able to place the putative markers for the base of the Maastrichtian in sequence, as well as certain other key fossil occurrences. Their scheme is as follows:

(Youngest)

- last occurrence of the nannofossil *Quadrum trifidum* [or *Tranolithus phacelosus* (= *orionatus*)].
- first occurrence of the ammonites *Pachydiscus (P.) neubergicus* and *Acanthoscaphites tridens*.
- last occurrence of the nannofossil *Broinsonia parca*.
- first occurrence of the ammonite *Hoploscaphites constrictus s.l.*
- first occurrence of the belemnite *Belemnella (B.) lanceolata*.
- last occurrence of the ammonite *Nostoceras (N.) hyatti*.
- last occurrence of the nannofossil *Reinhardtites anthophorus* (or *Eiffellithus eximus*).
- first occurrence of the ammonite *Nostoceras (N.) hyatti*.
- last occurrence of the planktonic foraminifer *Globotruncanita calcarata*.
- first occurrence of the planktonic foraminifer *Globotruncana falsostuarti*.
- first occurrence of the nannofossil *Reinhardtites levis*.

(oldest)

As they note, the first occurrence of the belemnite *Belemnella lanceolata* is widely taken to indicate the base of the Maastrichtian stage, and this is the definition adopted in the present work. Birkelund *et al.* (1984), in their review of the conclusions of the 1983 Copenhagen Meeting on Cretaceous stage boundaries, noted that it was 'widely accepted to keep the base of the Maastrichtian close to the appearance of *Belemnella lanceolata*, as this datum is so well-defined and widely accepted in the Boreal realm. However, there is a strong need for finer correlation of this boundary level with the succession in the Tethyan Realm possibly by planktonic foraminifera or coccoliths'.

Since the work of Burnett *et al.* and the partial achievement of the needs expressed at the Copenhagen Meeting (see also Schönfeld & Burnett 1991, Kennedy *et al.* 1992, Hancock *et al.* 1992, Hancock and Kennedy 1992) further refinements in correlation of the base of the Maastrichtian in the classic Boreal sense with Tethyan sequences have been achieved through the work of Burnett, Kennedy & Ward (1992), Hancock *et al.* (1993), Hancock & Kennedy (1992) and Ward & Kennedy (1993). These results are summarized in Figure 12. Ward & Kennedy (1993) recognized a threefold ammonite zonation of the Maastrichtian, with a fourth zone of *Pseudokossmaticeras tercense* that was possibly in part Campanian, in part Maastrichtian. Taking the base of the Maastrichtian at the first appearance of *Belemnella lanceolata*, the work of Hancock & Kennedy (1992) and Hancock *et al.* (1992) demonstrate that *Pachydiscus (P.) epiplectus*, *Hoploscaphites constrictus* and *P. (P.) neubergicus* first occur within a very narrow interval, such that the base of the Boreal *lanceolata* Zone and Tethyan *epiplectus* Zone are coeval, within the current limits of biostratigraphic correlation.

For subdivisions of the Maastrichtian we use Lower and Upper Substages, as is widely accepted by workers in the Boreal Realm, the base of the Upper Maastrichtian lying at the base of the *Belemnitella junior* Zone (Fig. 12).

Anapachydiscus fresvillensis (index species of the second zone of the Maastrichtian of Ward & Kennedy 1993) first occurs in the *junior* Zone in the Netherlands (Kennedy 1987). The base of the Boreal *junior* Zone and Tethyan *fresvillensis* Zone are coeval, within current limits of biostratigraphic correlation. *Anapachydiscus terminus*, index of the highest Tethyan Maastrichtian ammonite zone, is now known from the Boreal *casimirovensis* Zone (as *Anapachydiscus* aff. *fresvillensis* of Birkelund 1993 in Denmark, and, subsequently, in the Netherlands (Jagt, in press)). For a more refined division

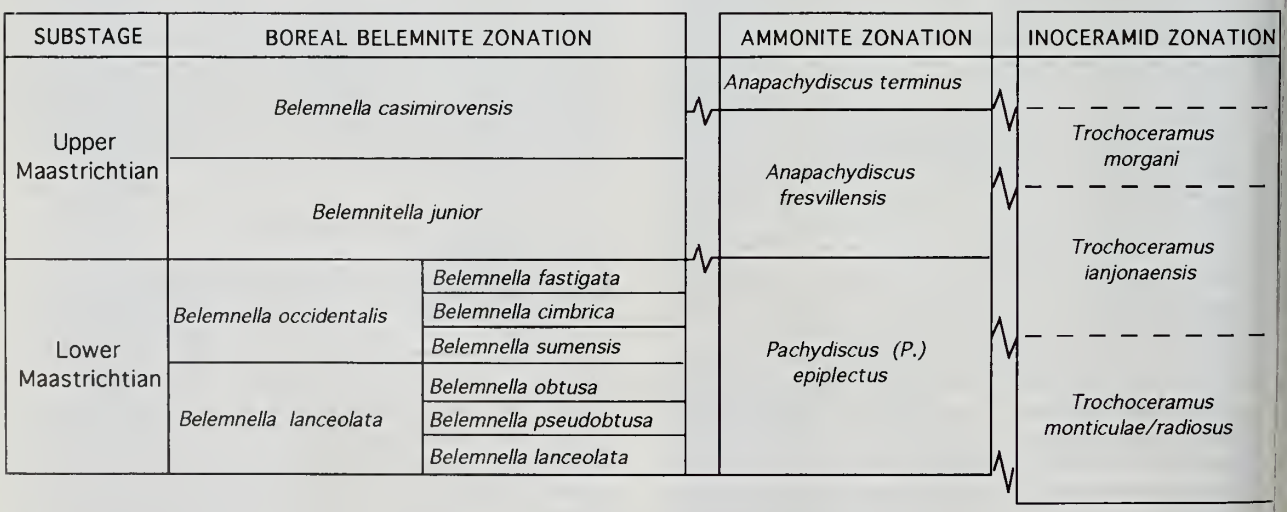


Fig. 12 Biostratigraphic zonation schemes for the Maastrichtian based on belemnites, ammonites and inoceramid bivalves, and their correlation.

of the Lower Maastrichtian reference will be made to the zonation of Schulz (1979: fig. 12).

Good palaeontological dating and correlation between the isolated jebels is very limited. Within each jebel there is evidence of sedimentation having taken place on an uneven sea-floor and relativily rapid changes of thickness and facies are sometimes visible by casual inspection. Larger benthonic foraminifera are often abundant but apparently controlled in their distribution by palaeoenvironment. Further careful collecting would be necessary before their stratigraphical potential is realized. Therefore, here we use evidence from the ammonite, inoceramid bivalve and echinoid faunas, together with inferred sea-level changes.

Ammonite biostratigraphy. The small number of late Cretaceous ammonites from the United Arab Emirates-Oman borders region (Kennedy, this volume) provide us with some constraints on the age of the succession. More weight has been placed on the pachydiscids than the heteromorphs, largely because they are better preserved.

The sections at Jebel Huwayyah include at least three ammonite horizons. The first and lowest contains an unidentified species of *Pachydiscus*, which was discovered at the top of the sand and conglomerate sequence of the Qahlah Formation, just below the *Loftusia*-rich beds, and only indicates a late Upper Cretaceous age.

The *Loftusia*-rich beds themselves have yielded the greatest number of ammonites, including *Pachydiscus (Pachydiscus) dossantoi* (Maury, 1930), *Lewyites ambindense* (Collignon, 1971), *Nostoceras (Nostoceras) major* Kennedy & Cobban, 1993, *Nostoceras (Nostoceras)* sp., and a *Libycoceras* sp. (not described; photograph only seen). The implied ages of these ammonites are somewhat contradictory. *Pachydiscus (P.) dossantoi* (Maury, 1930) is imprecisely dated within the Maastrichtian but occurs in the highest of three ammonite horizons in the Nkporo Shale of south-eastern Nigeria (Zaborski, 1985). At that locality it is closely associated with the inoceramids *Trochoceramus ianjonaensis* (Sornay) and *Endocostea coxi* (Reyment), which indicate a late Lower Maastrichtian to early Upper Maastrichtian age. *Lewyites ambindense* (Collignon, 1971) is known only from the lower Upper Maastrichtian, *fresvillensis* Zone. *Nostoceras (Nostoceras) major* Kennedy & Cobban, 1993 is Upper, but not uppermost, Maastrichtian, with an inferred *fresvillensis* Zone age. The presence of *Lewyites ambindense* and *Nostoceras (Nostoceras) major* imply a lower Upper Maastrichtian, *fresvillensis* Zone age. However, there are also two species that suggest an earlier age for at least part of the unit; *Nostoceras (Nostoceras)* sp. is uppermost Campanian or lower Lower Maastrichtian in age, and a specimen of *Libycoceras*, now in the Arab Emirates University Museum, has a bifid outer saddle indicative of the earliest of the three *Libycoceras* horizons described by Zaborski (1982) from Nigeria, and a late Campanian age. The age of the *Loftusia*-beds could therefore be as old as late Campanian or as young as early Upper Maastrichtian.

In the northwestern part of the outcrop at Jebel Huwayyah, close to where it is cut by the road, the lower part of the Simsima Formation yielded *Pachydiscus (Pachydiscus) neubergicus neubergicus* (Hauer, 1858), and *Lewyites ambindense* (Collignon, 1971). *Pachydiscus (P.) neubergicus neubergicus* (Hauer, 1858) implies a lower Lower to lower Upper Maastrichtian, *epiplectus* and *fresvillensis* Zones age. As pointed out above, *Lewyites ambindense* (Collignon) is known only from the lower Upper Maastrichtian.

A specimen of *Desmophyllites diphylloides* (Forbes, 1846) was found in bed 21 at Jebel Rawdah, section 2, well up in the Simsima Formation. However, the species is not age diagnostic, and its known range is Santonian to Upper Maastrichtian, *fresvillensis* Zone, and possibly higher. However, from Jebel Rawdah section 1, from scree almost certainly derived from the top of bed 4, we found a specimen *Brahmaites (Anabrahmaites) vishnu* (Forbes, 1846). The few well-dated specimens of this species are Upper Maastrichtian, *fresvillensis* Zone, and possibly younger in age.

In the basal transgressive calcarenite shell bed beneath the sands and conglomerates of the Qahlah Formation at Jebel Aqabah a *Glyptoxoceras* sp. was recovered. However, the genus is not age diagnostic and ranges from Santonian to upper Upper Maastrichtian. At Jebel Buhays, section 2, a *Libycoceras* sp. was found in the basal conglomerate of the Qahlah Formation. *Libycoceras* species first appear in the Upper Campanian and may range into the Lower Maastrichtian (Zaborski, 1982).

The basal beds of the Simsima Formation at Jebel Buhays, section 1, yielded a specimen of *Pachydiscus (P.) dossantoi* (Maury, 1930) which suggests a 'mid-Maastrichtian' age, presumably not very different to the *Loftusia*-rich beds at Jebel Huwayyah.

In conclusion then, the meagre ammonite data that we have suggests that the basal transgressive sands and conglomerates are late Campanian to 'mid-Maastrichtian' in age, whereas the main carbonate deposits of the Simsima Formation are of early Upper Maastrichtian, *fresvillensis* Zone, age. At Jebel Huwayyah the *Loftusia*-rich horizons may be as old as late Campanian or as young as early Upper Maastrichtian, *fresvillensis* Zone. We do not know whether or not sedimentation continued to the end of the Maastrichtian.

Inoceramid biostratigraphy. Inoceramid biostratigraphy has been based on what appear to be evolving lineages, often expressed as the ranges of subspecies. These are usually defined as the timespan of particular 'morphs' within an evolving species, although short-term biological events, such as the widespread 'flood' of a particular species or subspecies, are also important. Both methods can provide useful biostratigraphical data.

In recent years much progress has been made on integrating biostratigraphic data derived from Upper Cretaceous inoceramids and other fossil groups with data from sequence stratigraphy. Of all the Upper Cretaceous stages, however, the inoceramid biostratigraphic scheme for the Maastrichtian is the least well-established.

Species of the genus *Trochoceramus* hold the most promise for establishing a sound Maastrichtian biostratigraphy, since they apparently represent a relatively simple evolutionary lineage. *Trochoceramus* species have a somewhat rounded shell outline, with their umbones set back from the anterior, and have evenly spaced, rounded, comarginal ribs and distinctive radial ribs. The earliest species is narrow, with a regularly curving shell, but later species have a more convex shell, which is narrow in the early stages, but then undergoes a significant change in coiling direction, markedly increasing the relative volume of the mantle cavity. A similar change is also observed in the earlier genus *Cremnoceramus*.

Here we recognize three successive inoceramid faunas of *Trochoceramus* which can be used to zone the Maastrichtian. The lower division is characterized by the narrow, regularly

curved species *Trochoceramus* cf. *monticulae* (Fugger & Kastner) (?= *Trochoceramus radiosus* (Quaas)). These flat forms first occur in very late Campanian strata (e.g. in the Nacatoch Sand of Navarro County, Texas, U.S.A. (Stephenson 1941, pl. 13, fig. 3), and from Ammoniten Berg in the western Egyptian desert, apparently co-occuring with *Libycoceras ismaeli* (Quaas, 1902). However, the species becomes much more widespread in the lower part of the Lower Maastrichtian (Dhondt, 1983).

The middle division is characterized by a more convex species of *Trochoceramus, T. ianjonaensis* (Sornay), its convexity arising from a sharp change in shell curvature following an initial flattish stage. Such forms are known from Madagascar, where they have been dated as 'lower' Maastrichtian (Besairie 1972), although the ammonites listed suggest levels well into the Upper Maastrichtian as defined here. They are also known both from the Calabar district of Nigeria, where they are 'mid'-Maastrichtian, and the St. Lucia Formation of Zululand, Republic of South Africa, where they almost certainly extend into the Upper Maastrichtian. Finally, they are also reported from Libya, but apparently not associated with ammonites.

The upper division is characterized by *Trochoceramus morgani* (Sornay). It is of Upper Maastrichtian age and, so far, has only been recognized from the Calcaire à Baculites of the Cotentin Peninsula, France. *T. morgani* clearly differs from *T. ianjonaesis* by the smaller average size of the initial flat part of the shell (this average is 67% of the average size in *T. ianjonaensis*). Put another way, *T. ianjonaensis* includes forms with large and small initial shells, whereas *T. morgani* includes only specimens with small initial shells. Because this reduction in size of the initial flat portion of the shell has not been recognized in *Trochoceramus* from the Republic of South Africa, it is uncertain whether this size reduction represents a genuine world-wide change in the lineage or simply a geographical variation. A tentative biostratigraphic scheme for the Maastrichtian based on inoceramid bivalves and compared with the cephalopod biochronology is presented in Fig. 12.

Although inoceramid bivalves are proving useful for the division of the Maastrichtian they occur only rarely in the Upper Cretaceous deposits of the U.A.E. and Oman. We have discovered them at only three horizons, and so far only the material from Jebel Rawdah is at all well-preserved. Furthermore, none of this material includes species of *Trochoceramus*.

The lowest horizon includes only a fragment indeterminate at generic level, which was recovered from the conglomerate series below the *Loftusia*-beds at Jebel Huwayyah.

At the second horizon, in the basal transgressive shell bed of the Simsima Formation at Jebel Bu Milh, we found a single large fragmentary specimen of '*Platyceramus*' sp. This genus occurs in some abundance in the Maastrichtian succession of the St Lucia Formation in the Republic of South Africa, where it is common in the Lower Maastrichtian, but also seems to be dominant in the uppermost inoceramid horizon of that formation. A rather poorly preserved fragment of *Endocostea* cf. *bebahoaensis* comes from the *Loftusia*-beds at Jebel Huwayyah. It is not sufficiently well preserved to be dated better than Campanian or Maastrichtian.

The highest of the three levels, some way up the Simsima Formation at Jebel Rawdah, has yielded the most important inoceramid fauna. At Jebel Rawdah, section 1, just below the base of the more massive, well-cemented limestones (base of bed 5) *Endocostea (Cataceramus) semaili* sp. nov. occurs. This is most comparable with specimens from Nagoryany, Ukraine, and indicates a 'mid-Maastrichtian' horizon. Drs Skelton and Nolan also collected this species, together with *Endocostea* (*Endocostea*) cf. *coxi*, *Endocostea* sp. and '*Endocostea*' *bebahoaensis*, from the south-western part of the jebel at the same locality and possibly the same horizon as the ammonite *Pachydiscus (P.) neubergicus neubergicus*. *Endocostea coxi* occurs with *Trochoceramus ianjonaensis* in Nigeria and Zululand, while '*Endocostea*' *bebahoaensis* occurs with the same *Trochoceramus* in Madagascar, but is known to be long-ranging (it occurs in the Upper Maastrichtian at Cotentin, France). The inoceramids from Jebel Rawdah imply an early Upper Maastrichtian age, thus giving support to the age suggested by the ammonites from the same horizon.

Echinoid biostratigraphy. Although useful biostratigraphically for division of late Cretaceous–Palaeocene strata in the Boreal realm, echinoid distribution in Tethyan carbonate sequences is at present too poorly known to provide reliable dating of the succession. Furthermore, the environmental constraints of most species makes them highly restricted in their occurrence, and thus of limited value. However, our work has identified two biostratigraphically useful species lineages, *Hemipneustes* spp. and *Hattopsis* spp.

There are three species of *Hemipneustes* which differ in the relative elevation of the test, sharpness of the anterior sulcus and position of the apical disc. At Jebel Rawdah the lowest beds contain the flattest species, *H. persicus* Cotteau and Gauthier, and this species has a relatively broad and shallow anterior sulcus. Above this level, and possibly co-occurring for a short interval, comes *H. arabicus*, a species that is equally flat in profile but with a narrower and more sharply defined anterior sulcus. Higher beds contain an elevated species of *Hemipneustes*, *H. compressus*, and the relative elevation of the test increases up the succession, so that in the upper half of the Simsima Formation, *Hemipneustes compressus* begins to develop a strong apical elevation and narrower frontal groove, resembling the boreal species *H. striatoradiatus*.

The oldest species, *Hemipneustes persicus*, occurs (as *H. sardanyolae* Vidal) in the late Campanian of Spain. *H. arabicus* is endemic to this area, but the highest species, *H. compressus*, is known from the Maastrichtian of the Mari Hills, West Pakistan, where, unfortunately, the precise dating of the beds remains uncertain. At Jebel Rawdah, the replacement of *H. persicus* by *H. arabicus* seems to take place within the Upper Maastrichtian, according to the evidence of the ammonites and inoceramids.

The second biostratigraphically useful lineage comprises the two species of *Hattopsis*. At Jebel Faiyah, two species succeed one another, with *H. paucituberculatus* predating *H. sphericus*. This is useful for local correlation, since it is *H. paucituberculatus* that occurs at the base of the Simsima Formation at Jebel Buhays and *H. sphericus* that occurs near the base of the Simsima Formation at Jebel Rawdah. This then implies that the base of the Simsima Formation is not strictly contemporaneous between jebels.

Finally, it is noteworthy that the basal bed in the *Loftusia*-rich unit at Jebel Huwayyah yields a distinct suite of echinoids seen at no other jebel, including the holectypoid *Coptodiscus*. *Coptodiscus* is known from the late Campanian of Arabia

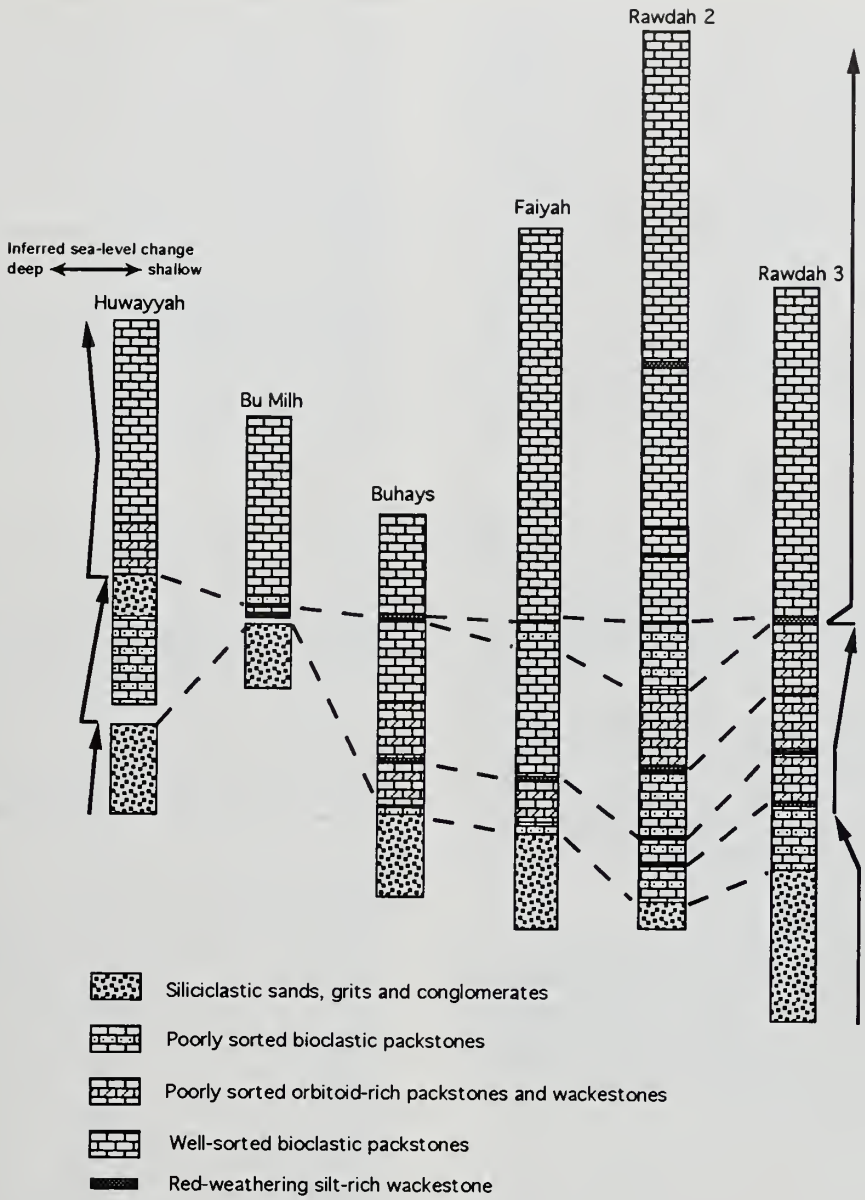


Fig. 13 Tentative correlation between jebels with inferred sea-level curves.

(Kier 1972) and from a presumed similar 'Senonian' horizon in southern Iran.

Global Sea-level curves. In broad terms the stratigraphic successions in the five jebels described here follow the same pattern, but in detail, precise correlation remains difficult, due to rapid shifts in facies and bed thickness across even small areas (Figs 6, 13). Sedimentation upon the Semail Nappe and Hawasina Group follows a typical transgressive pattern, often with massive boulder beds of serpentinite at the base overlain by arenitic and then calc-arenitic sediments, all deposited in shallow or nearshore marine environments. The lower clastic facies of conglomerates, sands and gravels are commonly included in the Qahlah Formation, whereas the sediments above, which are essentially bioclastic calcarenites, form the Simsima Formation. There is no reason to suppose, however, that the change from boulder beds and essentially quartz clastics upwards into calcarenites took place at the same time in all the sections we have examined.

The general deepening and shallowing cycles that can be recognized within individual sections allow a means of correlation. In all sections the initial coarse clastics of the Qahlah Formation are abruptly terminated, presumably marking the submersion of the ophiolitic complex within the region. This allowed carbonate production to dominate. For most of the Simsima Formation deposition appears to have more-or-less kept pace with subsidence so that sea-level remained around wave-base.

Furthermore, at Jebel Buhays, Jebel Faiyah and Jebel Rawdah there are conspicuous reddened beds and partings that probably contain land-derived iron oxides, which are a common constituent of lateritic soils formed on exposed

ophiolite. These red partings and thin beds presumably formed when lateritic soils were eroded and periodically flushed out to sea in run-off after heavy rains. Some may mark minor fluctuations in sea-level. They are potentially traceable over a wide area and may be important for local correlation. The problem is that there are not the same number of iron-enriched bands currently recognized in the different sections, and it becomes problematic as to which of several alternative bands should be correlated. A tentative correlation is presented in Fig. 13. However, mineralogical and geochemical analyses of these bands is needed to establish whether any have distinctive signatures.

The Cretaceous part of the section at Jebel Rawdah is topped by a limestone conglomerate apparently made up of eroded fragments of the Simsima Formation and including large chunks of rudists. This is in turn overlain by Lower Tertiary limestones. The lack of rounding and poor sorting of the clasts in the limestone conglomerate are probably indicative of subaerial erosion and deposition but we have no way of more accurately dating this period of emergence. It lies somewhere between late Maastrichtian and early Tertiary.

Flexer & Reyment (1989) identified two late Cretaceous transgressive events affecting the Arabo-Nubian shield: one in the late Campanian–early Maastrichtian, and the other in the late Maastrichtian. Although local tectonic events, associated with the ophiolite emplacement, may have had a profound effect on the local sea-level signature, it is tempting to associate the initial submergence of the ophiolitic islands and the sands and conglomerates of the Qahlah Formation with the late Campanian–early Maastrichtian transgression, and the later flooding of these beds and initiation of carbonate platform deposition with the second of these major sea-level transgressions in the late Maastrichtian. The end of the Cretaceous saw a major drop in sea-level.

Summary. Combining the evidence from ammonites, inoceramid bivalves, echinoids and global sea-level curves we conclude that the basal siliciclastic beds of the Qahlah Formation are of latest Campanian age. At Jebel Huwayyah, the *Loftusia*-rich levels of the Qahlah Formation probably encompass Lower to early Upper Maastrichtian. Finally, the Simsima Formation appears to be early Upper Maastrichtian, *fresvillensis* Zone or later.

REFERENCES

Ali, M.S.M. 1989. Late Cretaceous echinoids from Gebel El Rowdah, Hatta area, U.A.E. *Neues Jahrbuch für Geologie, Paläontologie und Mineralogie Abhandlungen*, **177**: 393–412.

—— 1992a. Additional echinoids from the late Maastrichtian (Cretaceous) of Gebel El Rowdah, Oman-United Arab Emirates. *Neues Jahrbuch für Geologie und Paläontologie Monatschefte*, **1992 (2)**: 65–74.

—— 1992b. A new genus and species of regular echinoid from the late Cretaceous of Gebel El Rowdah, Hatta area, Oman-U.A.E. *Journal of Paleontology*, **66**: 693–696.

Alsharhan, A.S. & Nairn, A.E.M. 1990. A review of the Cretaceous formations in the Arabian Peninsula and Gulf, part III, Upper Cretaceous (Aruma Group) stratigraphy and paleogeography. *Journal of Petroleum Geology*, **13**: 247–266.

—— & —— 1994. Carbonate platform models of Arabian Cretaceous resevoirs. *In* J.A. Toni Simo, R.W. Scott & J.P. Masse (editors), Cretaceous carbonate platforms. *American Association of Petroleum Geologists*, Memoir 56: 173–184.

Besairie, H. 1972. Géologie de Madagascar. 1, Les Terrains sédimentaires. *Annales géologiques de Madagascar*, **35**: 1–463, pls 1–89.

Birkelund, T., Hancock, J.M., Hart, B.M., Rawson, P.F., Remane, J., Robaszynski, F., Schmid, F. & Surlyk, F. 1984. Cretaceous stage boundaries proposals. *Bulletin of the Geological Society of Denmark*, **33**: 3–20.

Burnett, J.A., Hancock, J.M., Kennedy, W.J. & Lord, A.R. 1992. Macrofossil, planktonic foraminiferal and nannofossil zonation at the Campanian/Maastrichtian boundary. *Newsletters on Stratigraphy*, **27**: 157–172.

——, **Kennedy, W.J. & Ward, P.D.** 1992. Maastrichtian nannofossil biostratigraphy in the Biscay region (southwestern France, northern Spain). *Newsletters on Stratigraphy*, **26**: 145–155.

Carter, H.J. 1852. *Memoir on the geology of the southeast coast of Arabia*. 76 pp., 1 pl., Bombay.

Christensen, W.K. 1990. Upper Cretaceous belemnite stratigraphy of Europe. *Cretaceous Research*, **11**: 371–386.

Clegg, E.L.G. 1933. Echinoids from the Persian Gulf. *Memoirs of the Geological Survey of India; Palaeontologia Indica*, (New Series) **22** (1): 35 pp.

Collignon, M. 1971. *Atlas des fossiles caracteristiques de Madagascar (Ammonites); XVII* (Maastrichtien). Service géologique, Tananarive. iv + 44 pp., pls 640–658.

Dhondt, A.V. 1983. Campanian and Maastrichtian inoceramids: a review. *Zitteliana*, **10**: 689–701.

Duncan, P.M. 1865. A description of the Echinodermata from the strata on the southeastern coast of Arabia and at Bagh on the Nerbudda, in the collection of the Geological Society. *Quarterly Journal of the Geological Society, London*, **21**: 349–363.

Flexer, A. & Reyment, R.A. 1989. Note on Cretaceous transgressive peaks and their relation to geodynamic events for the Arabo-Nubian and the North African Shields. *Journal of African Earth Sciences*, **8**: 65–73.

Forbes, E. 1846. Report on the fossil Invertebrata from southern India collected by Mr Kaye and Mr. Cunliffe. *Transactions of the Geological Society of London*, (2) **7**: 97–174, pls 7–19.

Ghalib M.A. el Asa'ad 1989. Solitary Maastrichtian corals from the Aruma Formation of Saudi Arabia. *Mesozoic Research*, **2**: 29–39.

—— 1990. Maastrichtian species of the coral genus *Cunnolites* from Saudi Arabia. *Journal of African Earth Science*, **10**: 633–642.

Glennie, K. 1977. Outline of the geology of Oman. *Memoires Hors Série. Société géologique de France*, **8**: 25–31.

——, **Bouef, M., Clark, M.W., Moody-Stuart, M., Pilaar, W.F. & Reinhardt, B.M.** 1974. Geology of the Oman Mountains. *Verhandelingen van het Koninklijk Nederlandisch Geologisch Mijnbouwkundig Genootschap*, **31**: 1–423.

Hancock, J.M. & Kennedy, W.J. 1992. The high Cretaceous ammonite fauna from Tercis, Landes, France. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique*, **63**: 149–209, 20 pls.

——, **Peake, N.B., Burnett, J.A., Dhondt, A.V., Kennedy, W.J. & Stokes, R.B.** 1992. High Cretaceous stratigraphy at Tercis, southwest France. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique*, **63**: 133–148.

——, **Russell, E.E., Taylor, R.H. & Gale, A.S.** 1992. The relative stratigraphic position of the foraminiferal and belemnite standards for the Campanian-Maastrichtian boundary. *Geological Magazine*, **129**: 787–792.

Hughes-Clarke, M.W. 1988. Stratigraphy and rock-unit nomenclature in the oil-producing area of interior Oman. *Journal of Petroleum Geology*, **11**: 5–60.

Kennedy, W.J. 1987. The ammonite faunas of the type Maastrichtian, with a revision of *Ammonites colligatus* Binkhorst, 1861. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique*, **56**: 151–267, 37 pls.

—— & **Cobban, W.A.** 1993. Maastrichtian ammonites from the Corsicana Formation in northeastern Texas, *Geological Magazine*, **130**: 57–67.

——, —— & **Scott, G.R.** 1992. Ammonite correlation of the uppermost Campanian of Western Europe, the U.S. Gulf Coast, Atlantic Seaboard and Western Interior, and the numerical age of the base of the Maastrichtian. *Geological Magazine*, **129**: 497–500.

—— & **Hancock, J.M.** 1993. Upper Maastrichtian ammonites from the Marnes de Nay between Gan and Rébénacq (Pyrénées-Atlantiques), France. *Géobios*, **26**: 575–594.

—— & **Simmons, M.D.** 1991, Mid-Cretaceous ammonites and associated macrofossils from the Oman Mountains. *Newsletters on Stratigraphy*, **25**: 127–154.

Kier, P.M. 1973. Tertiary and Mesozoic echinoids from Saudi Arabia. *Smithsonian Contributions to Paleobiology*, **10**: i–iii, 1–242.

Lees, G.M. 1928. Geology and tectonics of Oman and parts of southeastern Arabia. *Quarterly Journal of the Geological Society of London*, **84**: 585–670.

Metwally, M.H.M. 1992. Late Cretaceous (Maastrichtian) bivalves from the northwestern flank of the Oman Mountains, UAE. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **184**: 123–139.

Obradovich, J. 1993. A Cretaceous time scale. *Geological Association of Canada Special Paper*, **39**: 379–396.

Platel, J.P. & Roger, J. 1989. Evolution géodynamique du Dhofar (Sultanat d'Oman) pendant le Crétacé et le Tertiaire en relation avec l'ouverture du

golfe d'Aden. *Bulletin de la Société géologique de France*, Serie 8, **5**: 253–263.
Quaas, A. 1902. Beitrag zur Kenntnis der Fauna der obersten Kreidebildunge in der libyschen Wüste (Overwegschichten und Blatterthon). *Palaeontographica*, **30**: 153–366, 10 pls.
Robertson, A.H.F., Searle, M.P. & Ries, A.C. (eds). 1990. The geology and tectonics of the Oman region. *Geological Society of London, Special Publication*, no. 49, 845 pp.
Roger, J., Platel, J.P., Cavelier, C. & Bourdillon de Grissac, C. 1989. Données nouvelles sur la stratigraphie et l'histoire géologique du Dhofar (Sultanat d'Oman). *Bulletin de la Société géologique de France*, Serie 8, **5**: 265–277.
Roman, J., Roger, J., Platel, J.-P. & Cavelier, C. 1989. Les Echinoides du Cretacé et du Paléogene du Dhofar (Sultanat d'Oman) et les relations êntre les bassins de l'océan Indien et de la Mediterranée. *Bulletin de la Société géologique de France*, Series 8, **5**: 279–286.
Schönfeld, J. & Burnett, J. 1991. Biostratigraphical correlation of the Campanian/Maastrichtian boundary: Lägerdorf-Hemmoor (northwestern Germany) DSDP sites 548A, 549 and 531 (eastern North Atlantic) with particular reference to palaeobiogeography and palaeoceanographical implications. *Geological Magazine*, **128**: 479–503.
Schulz, M.G. 1979. Morphometrischvariationsstatistisch Untersuchungen zur Phylogenie der Belemniten-Gattung *Belemnella* in Unter-Maastricht NW Europas. *Geologisches Jahrbuch*, **A47**: 31–57, 12 pls.
Seitz, O. 1970. Über einige Inoceramen aus der oberen Kreide. 2. Die Muntliger Inoceramenfauna und ihre Verbreitung im OberCampan und Maastricht. *Beihefte geologisches Jahrbuch* **86**: 105–171.
Skelton, P.W., Nolan, S.C. & Scutt, R.W. 1990. The Maastrichtian transgression onto the northwestern flank of the proto-Oman mountains, sequences of rudist-bearing beach to open shelf facies. *In*, Robertson, A.H.F., Searle, M.P. & Ries, A.C. (eds), The geology and tectonics of the Oman region. *Geological Society of London, Special Publication*, no. 49: 521–547.
Smith, A.B., Simmons, M. & Racey, A. 1990. Cenomanian echinoids, larger foraminifera and calcareous algae from the Natih Formation, central Oman Mountains. *Cretaceous Research*, **11**: 29–69.
Stephenson, L.W. 1944. The larger invertebrate fossils of the Navarro Group of Texas. *University of Texas Bulletin*, **4101**: 16–41.
Ward, P.D. & Kennedy, W.J. 1993. Maastrichtian ammonites from the Biscay region (France, Spain). *Paleontological Society Memoir*, **34**: 58 pp.
Zaborski, P.M.P. 1982. Campanian and Maastrichtian sphenodiscid ammonites from southern Nigeria. *Bulletin of the British Museum (Natural History), Geology Series*, **36** (4): 303–332.

APPENDIX

Macrofossils collected in the United Arab Emirates/Oman border region. Echinoids identified by A.B. Smith, nautiloids, bivalves and gastropods by N.J. Morris, P.W. Skelton and R.J. Cleevely, ammonites by W.J. Kennedy, corals by J. Darrell and B.R. Rosen, bryozoans by P.D. Taylor and brachiopods by E.F. Owen. Locality details are given in the main text: bed numbers refer to those shown in figures 5–11. Numbers in square brackets after each name refer to the number of specimens collected.

Jebel Buhays, Section 1

Top of Bed 4. Echinoids: *Arnaudaster cylindriformis* sp. nov. [1]; *Circopeltis? emiratus* sp. nov. [1]. **Ammonite:** *Pachydiscus dossantoi* (Maury) [1].

Bed 10. Echinoids: *Hemipneustes* sp. [1]; *Coenholectypus* cf. *baluchistanensis* (Noetling) [1].

Bed 11. Bivalves: *Dictyoptychus morgani* (Douvillé) [2]; **Gastropods:** *Acteonella crassa* (Dujardin) [6].

Bed 12, base. Echinoids: *Goniopygus arabicus* sp. nov. [1]; *Hattopsis paucituberculatus* sp. nov. [1 fragment]. **Coral:** *Hydnophoraraea* sp. [1]. **Bivalves:** *Scabrotrigonia* sp. [3].

Bed 15. Echinoid: *Codiopsis lehmannae* sp. nov. [1]. **Bivalve:** *Hippurites* cf. *cornucopiae* Defrance [6].

Lowest part of Simsima Formation (beds 4–10) – mostly collected loose. **Echinoids**: Rhabdocidarid, gen. et sp. indet. [1]; *Prionocidaris morgani* (Gauthier) [2]; cidarid spines [2]; *Heterodiadema buhaysensis* sp. nov. [2]; *Orthopsis miliaris* (d'Archiac) [10]; *Salenia nutrix* Peron & Gauthier [5]; *Goniopygus arabicus* sp. nov. [22]; *Glyphopneustes hattaensis* Ali [41]; *Hattopsis paucituberculatus* sp. nov. [11]; *Noetlingaster paucituberculatus* (Noetling) [3]; *Phymosoma hexoaporum* Lambert [13]; *Actinophyma spectabile* Cotteau & Gauthier [4]; *Plistophyma asiaticum* Gauthier [3]; *Circopeltis? emiratus* sp. nov. [1]; *Coenholectypus inflatus* (Cotteau & Gauthier) [8]; *Coenholectypus* cf. *baluchistanensis* (Noetling) [3]; '*Globator*' *bleicheri* (Thomas & Gauthier) [96]; *Conulus douvillei* (Cotteau & Gauthier) [19]; *Vologesia rawdahensis* Ali [3]; *Pygurostoma morgani* Cotteau & Gauthier [26]; *Petalobrissus* cf. *setifensis* (Cotteau) [1]; *Nucleopygus magnus* sp. nov. [27]; *Arnaudaster cylindriformis* sp. nov. [5]; *Hemipneustes* sp. indet. (fragments) [3]; *Hemiaster hattaensis* Ali [4]. **Bivalves:** *Arca* sp. [1, bivalved]; *Cucullaea* sp. A [3, 2 bivalved]; '*Modiolus*' cf. *capitatus* Zittel [3, bivalved]; *Mytilus* sp. nov? [1, bivalved]; *Modiolus* aff. *typicus* Forbes [3, bivalved]; *Neithea regularis* (Schlotheim) [33]; *Spondylus* sp. C [1]; *Spondylus* sp. D [1]; *Ctenoides* aff. *scaberrima* (Stolizcka) [14]; ?*Osculopha* sp. [1]; ?*Gyropleura* sp. [1]; ?*Pycnodonte uncinella* (Leymerie) [8]; *Amphidonte pyrenaicum* (Leymerie) [2]; *Agerostrea ungulata* (Schlotheim) [4]; Eligmidae [6, bivalved]; ?*Tellinella* sp. [1]; *Glabrobournonia arabica* Morris & Skelton sp. nov. [12]; Tancrediidae cf. *Tatella* sp., sp. nov. [1]; *Clavagella* cf. *semisulcata* Forbes [2, bivalved]; *Pholadomya* sp. B [1, bivalved]. **Gastropods:** *Bathrotomaria* cf. *verdachellensis* (Forbes) [2]; *Calliomphallus* sp. [1]; *Angaria* sp. [1]; '*Tectus*' ex. gr. *rozeti* (d'Archiac) [7]; Umboniinae nov. gen. [9]; ?*Rhabdoconcha* sp. [1]; Turritellidae [2]; *Pyrazus* sp. [1]; *Campanile* sp. [8]; *Tylostoma incerta* (Forbes) [9]; Naticidae [1]; Strombidae, gen. nov., cf. *crassicostatus* (Noetling) [1]; Strombidae, gen. nov. [1]; Strombacea [3]; ?*Ovula expansa* d'Archiac & Haime [4]; Cypraeidae [1]; ?Tonnacea [1]; '*Volutilithes*' *dubia* Noetling [7]; ?*Volutoderma* sp. [4]; *Caricella* sp. [1]; Volutidae A [1]; Volutidae B [2]; Volutidae C [2]; Volutidae D [3]; Neogastropoda indet. [1]; *Acteonella crassa* (Dujardin) [4]; *Acteonella caucasica* Zekeli cf. *styriaca* Kollman [3]; *Acteonella* sp. cf. *A. borneensis* Nuttall & Leong [19]; *Acteonella caucasica* Zekeli subsp. nov. [7]; *Acteonella crassa* (Dujardin) [9]; *Neocylindrites* cf. *minutus* Sohl [3]; *Neocylindrites* sp. [1]; opisthobranch [2]. **Corals:** *Polytremacis* sp. [2]; *Aspidastraea* sp. [1]; *Cunnolites* sp. [4]; *Diploctenium* sp. [3]; *Hydnophoraraea* sp. [2]; *Paraplacocoenia orbignyana* (Reuss) [1]; cerioid colony [1]; phaceloid colony [1]; solitary form [1]. **Stromatoporoid**: massive stromatoporoid (bored by bivalves) [1]. **Sponge**: chaetetid [1]. **Bryozoan**: '*Onychocella*' sp. [1]. **Decapod crustaceans:** *Carcinerctes* sp. [3 carapaces, 5 limb segments]; crab carapace, species A [1]; crab carapace, species B [2]; claw, indet. [1].

Jebel Buhays Section 1a

Small hill 150 m to south of Jebel Buhays 1. Collected from scree, in rock fall from lowest 4 m of Simsima Formation (beds are steeply dipping and all loose material must be derived from the basal beds here).

Echinoids: *Heterodiadema buhaysensis* sp. nov. [1]; *Orthopsis miliaris* (d'Archiac) [7]; *Salenia nutrix* Peron & Gauthier [2]; *Goniopygus arabicus* sp. nov. [7]; *Glyphopneustes hattaensis* Ali [9]; *Phymosoma hexoaporum* Lambert [3]; *Actinophyma spectabile* Cotteau & Gauthier [1]; *Plistophyma asiaticum* Gauthier [3]; *Coenholectypus inflatus* (Cotteau & Gauthier) [3]; '*Globator*' *bleicheri* (Thomas

& Gauthier) [occurs]; *Conulus douvillei* (Cotteau & Gauthier) [occurs]; *Vologesia rawdahensis* Ali [2]; *Petalobrissus linguiformis* (Peron & Gauthier) [1]; *Nucleopygus magnus* sp. nov. [9]; *Hemipneustes* sp. [1]; *Hemiaster hattaensis* Ali [3]. **Bivalves:** *Cucullaea* sp. A [4]; *Barbatia* sp. [1]; *Lyriochlamys ternatus* (Münster) [6]; *Neithea regularis* (Schlotheim) [6]; *Agerostrea ungulata* (Schlotheim) [4]; ?*Pycnodonte uncinella* (Leymerie) [1, bivalved]; *Scabrotrigonia* sp. [8]; *Dictyoptychus morgani* Douvillé [1, lid]; *Glabrobournonia arabica* Morris & Skelton sp. nov. [2]; *Clavagella* cf. *semisulcata* Forbes [2]. **Gastropods:** *Tylostoma incerta* (Forbes) [2]; ?Strombidae, gen. nov. [1]; *Pseudomelania [Trajanella]* sp. cf. *conica* (Stolizcka) [2]; *Acteonella crassa* (Dujardin) [13]; *Acteonella* cf. *laevis laevis* (Sowerby) [6]; *Acteonella* cf. *borneensis* Nuttall and Leong [4]; *Neocylindrites* sp. cf *minutus* Stolizcka [1]. **Cephalopods:** *Cimomia* aff. *sowerbyana* (d'Orbigny) [1]; *Deltoidonautilus salisfilius* sp. nov. [1]. **Corals:** *Polytremacis* sp. [1]; *Favia* sp. cf. *'Diplocoenia' klogsdorfensis* Trauth [1]; *Barysmilia irregularis* (Reuss) [1]; *Cunnolites* sp. [1]; *Diploctenium* sp. [1]; cerioid colony [1]. **Sponge** [1].

Jebel Buhays 2

Collections made from the scree-slope. Here the bedding is very steep and material is derived from the lowest few metres of section only.

Echinoids: *Salenia nutrix* Peron & Gauthier [1]; *Goniopygus arabicus* sp. nov. [4]; *Coenholectypus inflatus* (Cotteau & Gauthier) [1]; *'Globator' bleicheri* (Thomas & Gauthier) [3]; *Conulus douvillei* (Cotteau & Gauthier) [3]; *Pygurostoma morgani* Cotteau & Gauthier [2]. **Bivalves:** *Dictyoptychus morgani* (Douvillé) [1]; *Glabrobournonia arabica* Morris & Skelton, sp. nov. [16]; **Ammonite:** *Libycoceras* sp. [1].

Jebel Buhays 3

Basal limestone (lowest 1m). Echinoids: *Goniopygus arabicus* sp. nov. [4]; *Nucleopygus magnus* sp. nov. [1].

Above first major red-weathering siltstone level. Echinoids: *Circopeltis emiratus* sp. nov. [2].

Loose. Echinoids: *Salenia nutrix* Peron & Gauthier [2]; *Hattopsis paucituberculatus* sp. nov. [2]; *Phymosoma hexoaporum* Lambert [1]; *'Globator' bleicheri* (Thomas & Gauthier) [1]. **Bivalves:** *Hippurites cornucopiae* Defrance [1]; ?*Biradiolites* aff. *baylei* Toucas [2].

Jebel Thanais

Lowest 4 m of Simsima Formation. Echinoids: *Heterodiadema buhaysensis* sp. nov. [1]; *Orthopsis miliaris* (d'Archiac) [1]; *Salenia nutrix* Peron & Gauthier [2]; *Goniopygus arabicus* sp. nov. [2]; *Glyphopneustes hattaensis* Ali [6]; *Hattopsis* sp. [1]; *Phymosoma hexoaporum* Lambert [3]; *Plistophyma asiaticum* Gauthier [2]; *Coenholectypus* cf. *baluchistanensis* (Noetling) [2]; *'Globator' bleicheri* (Thomas & Gauthier) [5]; *Conulus douvillei* (Cotteau & Gauthier) [8]; *Vologesia rawdahensis* Ali [1]; *Pygurostoma morgani* Cotteau & Gauthier [1]; *Nucleopygus magnus* sp. nov. [4]; *Hemiaster hattaensis* Ali [1]. **Bivalves:** ?*Barbatia* sp. A, cf. *B. morgani* (Douvillé) [2, bivalved]; *'Modiolus'* aff. *typicus* Forbes [1, bivalved]; *Neithea regularis* (Schlotheim) [2]; *Pycnodonte vesicularis* (Lamarck) [1, bivalved]. **Gastropods:** *Acteonella* sp. cf. *A. borneensis* Nuttall & Leong [1]; *Acteonella caucasica* Zekeli subsp. cf. *styriaca* Kollman [1]; *Acteonella caucasica caucasica* Zekeli [1]. **Corals:** *Cunnolites* sp. [1]; *Diploctenium* sp. [1]; *Moltkia isis* Steenstrup [1]; *Paraplacocoenia orbignyana* (Reuss) [1]; coarse meandroid colony [1]. **Bryozoan:** *'Onychocella'* sp. [1]. **Decapod crustacean:** limb segments [3].

Upper beds (equivalent to bed 15 of Jebel Buhays 1). Bivalves: *Hippurites cornucopiae* Defrance [1].

Loose in scree. Bivalves: *Cucullaea* sp. A [2 ,1 bivalved]; *'Modiolus'* aff. *typicus* Forbes [1, bivalved]; *Chlamys dujardeni* (Roemer) [1]; *Neithea regularis* (Schlotheim) [3]; *Spondylus* sp. E [1]; *Ctenoides* aff. *scaberrima* (Stolizcka) [2]; ?*Amphidonte* cf. *pyrenaicum* (Leymerie) [1]; ?*Osculopha* sp. [1]; Lucinidae gen. indet., sp. B [1, bivalved]; *Dictyoptychus morgani* (Douvillé) [1]; *Glabrobournonia arabica* Morris & Skelton, sp. nov. [1]; *Colveraia variabilis* Klinghardt [1]; *Vaccinites vesiculosus* (Woodward) [4]; *Lapeirousia* sp. [2]; *Pholadomya* sp. B [1, bivalved]. **Gastropods:** *Tylostoma incerta* (Forbes) [1]; *Acteonella crassa* (Dujardin) [5].

Jebel Aqabah

Excellent outcrop of the basal part of the marine sequence resting directly on serpentinized ultramafics.

Bed 1. Echinoids: *Hattopsis paucituberculatus* sp. nov. [1]; *'Globator' bleicheri* (Thomas & Gauthier) [2]; *Faujasia eccentripora* Lees [6 juveniles]. **Ammonite:** *Glyptotoxoceras* sp. [1].

Loose. Bivalves: ?*Pycnodonte uncinella* (Leymerie) [2]; *Dictyoptychus morgani* (Douvillé) [1]; ?*Biradiolites* aff. *baylei* Toucas [3]. **Gastropods:** *Acteonella crassa* (Dujardin) [2]. **Cephalopod:** *Cimomia* aff. *sowerbyana* (d'Orbigny) [1]. **Coral:** *Cunnolites* sp. [1].

Jebel Huwayyah, Section 1

Bed 1. Bivalves: ?*Acutostrea* sp. [*ca.* 10].

Bed 3. Bivalves: ?*Acutosrea* sp. [abundant].

Bed 7. Stromatoporoid [1].

Bed 9. Echinoids: *Faujasia eccentripora* Lees [6]; *Hemiaster* sp. cf. *H. hattaensis* Ali [1]. **Bivalves:** *Spondylus* sp. A [1]; *Vaccinites vesiculosus* (Woodward) [5]; ?*Granocardium* sp. [1]. **Gastropods:** ?*Tectus* sp. [1]; *Campanile* sp. [1]; *Amauropsina* aff. *bulbiformis* (J. de C. Sowerby) [1]; *'Ampullina* aff. *splendida'* (Deshayes) [3]. **Corals:** *Cunnolites* sp. [4]; cerioid colony (with *Lithophaga* borings) [1]. **Ammonite:** *Pachydiscus* sp. [1].

Beds 10–11. Echinoids: *Faujasia eccentripora* Lees [33]; *Hemiaster* sp. cf. *H. hattaensis* Ali [1]. **Bivalves:** *Endocostea* cf. *bebahoaensis* (Sornay) [1]; *Spondylus* sp. A [2]; *Plicatula hirsuta* Coquand [4]; ?*Acutostrea* sp. [6]; *Glabrobournonia arabica* Morris & Skelton, sp. nov. [1]; *Pholadomya?* sp. B [1]. **Gastropods:** cf. *Tylostoma incerta* (Forbes) [1]. **Corals:** *Cunnolites* sp. [2]; *Paraplacocoenia orbignyana* (Reuss) [1]; large trochoid solitary [1]; large flabellate solitary [1]; cerioid colonies (5 genera) [7]. **Ammonites:** *Pachydiscus dossantoi* (Maury) [1]; *Lewyites ambindense* (Collignon) [1]; *Nostoceras (Nostoceras) major* Kennedy & Cobban [1].

Beds 9–11 undifferentiated. Bivalves: *Torreites sanchezi* (Douvillé) [2] *Durania* form A [1].

Bed 13. Bivalves: *Durania* spp. [fragments].

Beds 14/15. Echinoids: *Coenholectypus inflatus* (Cotteau & Gauthier) [1]; *'Globator' bleicheri* (Thomas & Gauthier) [54]; *Pygurostoma morgani* Cotteau & Gauthier [3]; *Hemipneustes* sp. [1]. **Bivalves:** *Cucullaea* sp. A [1]; *Lyriochlamys ternatus* (Münster) [7]; *Neithea regularis* (Schlotheim) [8]; *Spondylus* sp. A. [2]; *Dictyoptychus morgani* (Douvillé) [1]. **Gastropods:** *Execochirsus* sp. [1]; *Campanile* sp. [1]; Cerithiidae [1]; *Tylostoma incerta* (Forbes) [6]; Strombacea [1]; ?Aporrhaidae [1]; Neogastropods [2]. **Ammonite:** *Pachydiscus dossantoi* (Maury) [1]. **Coral:** *Cunnolites* sp. [1].

Bed 16. Bivalves: *Pycnodonte vesicularis* (Lamarck) [2]; *Agerostrea ungulata* (Schlotheim) [12, bivalved].

Bed 17. Bivalves: *Lyriochlamys ternatus* (Münster) [1]; *Neithea regularis* (Schlotheim) [2]; *Scabrotrigonia* sp. [4]; *Durania* sp. [2]. **Gastropods:** *Bathrotomaria* sp. [1].

Bed 18, towards top of section. **Echinoids:** *Proraster geayi* Cottreau [7].

Loose. Echinoid: *Mecaster* sp.? [1]. **Bivalve:** ?*'Inoceramus'* sp. [1].

Jebel Huwayyah, Section 2

Bed 1. Echinoids: *Glyphopneustes hattaensis* Ali [1]; *Coptodiscus magniproctus* sp. nov. [2].

Beds 3–5. Echinoids: cidarid spine [1]; *Orthopsis* sp. [1]; *Salenia microprocta* sp. nov. [1]; ?*Hattopsis* sp. [1]; *Faujasia eccentripora* Lees [1]; *Hemiaster* sp. cf. *H. hattaensis* Ali [3]; *Mecaster* sp. [4]; *Proraster geayi* Cottreau [2]. **Bivalves:** *Dictyoptychus morgani* (Douvillé) [1]; **Corals:** *Cunnolites* sp. [27]; *Diploctenium* sp. [4]; *Placosmilia* sp. [22]. **Bryozoans:** cf. *Euritina lata* Canu [1]; '*Wilbertopora*' sp. [1]. **Decapod crustacean:** pincer [1]. **Brachiopods:** terebratulid gen. et sp. nov. [3]. **Ammonite:** *Nostoceras* sp. [1].

Bed 7. Bivalves: *Vaccinites vesiculosus* (Woodward); **Corals:** *Actinacis* sp. [3]; *Cladocora ?humilis* (Michelin) [7]; ?*Aspidastraea* sp. [1]; *Astraraea* sp. [3]; *Calamophylliopsis simonyi* (Reuss) [1]; *Paraplacocoenia orbignyana* (Reuss) [1]; cerioid colonies (3 genera) [4]; thamnasteroid colonies [4]; coarse meandroid colonies [5]; elongate-oval flat solitary corals [3]; flabellate solitary corals [2]; turbate solitary corals [10]; cylindrical solitary corals [3]. **Ammonite:** *Neancycloceras* sp. [1].

Loose in scree, but derived from Loftusia beds, beds 2–7 unless otherwise stated. **Echinoids:** *Prionocidaris*? *emiratus* sp. nov. [1]; *Coenholectypus inflatus* (Cotteau & Gauthier) [3] (probably derived from Simsima Formation above?). **Bivalves:** *Endocostea* cf. *bebahoaensis* (Sornay) [1]; *Lyriochlamys ternatus* (Münster) [8]; *Neithea regularis* (Schlotheim) [19]; *Neithea (Neithella) notabilis* (Munster) [1]; *Spondylus* sp. A [49, 19 bivalved]; *Spondylus* sp. B [12, 4 bivalved]; *Plicatula hirsuta* Coquand [23]; ?*Osculopha* sp. [4, 1 bivalved]; *Amphidonte pyrenaicum* (Leymerie) [10, 2 bivalved]; *Agerostrea ungulata* (Schlotheim) [1, bivalved]; ?Eligmidae indet. [1]; *Ctenoides* sp. [2]; *Chama noetlingi* [7]; *Biradiolites* aff. *baylei* Toucas [1]; *Glabrobournonia arabica* Morris & Skelton, sp. nov. [10]; *Semailia smithi* Morris & Skelton, sp. nov. [1]; *Vaccinites vesiculosus* (Woodward) [25]; *Pholadomya* sp. A, cf. *indica* Noetling [2]; *Pholadomya* sp. B [1, bivalved]. **Gastropods:** ?*Angaria* sp. [5]; Turbinidae sp. [5]; Turritellidae sp. [10]; ?*Pyrazus* sp. [3]; Cerithiidae sp. [1]; ?*Perrisoptera* sp. [7]; ?Naticidae sp. [7]; ?Fasciolariidae sp. [1]; Volutidae sp. A [1]; Volutidae sp. B [1]; ?Mitridae sp. [1]; neogastropods [2]; *Acteonella* sp. [1].

Jebel Rawdah, Section 1

Bed 2. Echinoid: *Petalobrissus* cf. *setifensis* (Cotteau) [1]. **Bivalves:** ?'*Modiolus*' cf. *capitatus* Zittel [1, bivalved]; *Cucullaea* sp. A [11]; *Lyriochlamys ternatus* (Münster) [2]; *Neithea regularis* (Schlotheim) [7]; *Pycnodonte vesicularis* (Lamarck) [1]; ?*Pycnodonte uncinella* (Leymerie) [7]; *Agerostrea ungulata* (Schlotheim) [1]; Indet. ribbed oyster [1]; *Scabrotrigonia* sp. [62, 7 bivalved]; *Durania* spp. [2]; *Glabrobournonia arabica* Morris & Skelton [4]; Tancrediidae, cf. *Tatella*, sp. nov. [2, bivalved]. **Gastropods:** *Acteonella* sp. cf. *borneensis* Nuttall & Leong [4]. **Corals:** *Cunnolites* sp. [7]; *Diploctenium* sp. [1].

Bed 3 (lower part) and top of Bed 2. Echinoids: *Orthopsis miliaris* (d'Archiac) [2]; *Salenia nutrix* Peron & Gauthier [2]; *Hattopsis sphericus* Ali [19]; *Noetlingaster paucituberculatus* (Noetling) [5, fragments]; *Coenholectypus* cf. *baluchistanensis* (Noetling) [1]; '*Globator*' *bleicheri* (Thomas & Gauthier) [49]; *Faujasia eccentripora* Lees [5]; *Zuffardia morgani* (Cotteau & Gauthier) [4]; *Petalobrissus* cf. *setifensis* (Cotteau) [17]; *Phymechinus?* sp. [fragment]. **Bivalves:** ?*Barbatia* sp. A, cf. *B. morgani* Douvillé [1, bivalved]; *Cucullaea* sp. A [4, 3 bivalved]; ?'*Mytilus*' *nitens* Forbes [1, bivalved]; '*Modiolus*' cf. *capitatus* Zittel [5, 4 bivalved]; *Pinna* sp. [3]; *Endocostea (Selenoceramus) semaili* sp. nov. [1]; *Lyriochlamys ternatus* (Münster) [3]; *Neithea regularis* (Schlotheim) [23]; Limidae [1]; *Plicatula hirsuta* Coquand [1]; *Pycnodonte vesicularis* (Lamarck) [6]; *Pycnodonte vesicularis* (Lamarck) var. *hippopodium* Nillson [1]; ?*Pycnodonte uncinella* (Leymerie) [10, 4 bivalved]; ?*Amphidonte* cf. *pyrenaicum* (Leymerie) [2]; *Scabrotrigonia* sp. [6, 2 bivalved]; Lucinidae sp. [1]; ?*Plagyoptychus* sp. [1]; *Dictyoptychus morgani* (Douvillé) [10]; *Glabrobournonia arabica* Morris & Skelton, sp. nov. [22]; *Durania* spp. [6 fragments]; ?Trapeziidae [1]; ?*Mesocallista* sp. [5, bivalved]; Tellininae [1]; ?Tancrediidae, cf. *Tatella*, sp. nov. [2]; *Clavagella* cf. *semisulcata* Forbes [6]; ?*Brechites* cf. *aspergilloides (Forbes)* [1]; *Pholadomya* sp. B [1]. **Gastropods:** *Calliomphalus* sp. [4]; ?*Angaria* sp. [2]; ?*Tectus* sp. [3]; ?*Pseudoliotina* sp. [1]; ?Umboniinae, gen. nov. [64]; euomphalid gen. nov. [6]; ?*Rhabdoconcha* sp. [1]; ?Turritellidae [2]; Vermetidae or Siliquariidae [1]; Cerithiidae [7]; Cypraeidae, sp. [4]; ?Cypraeidae. [3]; ?Volutacea [1]; *Ampullina* aff. '*splendida*' (Deshayes) [4]; *Tylostoma incerta* (Forbes) [2]; Mesogastropod [2]; ?*Anchura* sp. [3]; ?Aporrhaidae [1]; Hipponicidae [3]; ?Fasciolariidae [1]; ?Volutidae [16]; ?Buccinacea [7]; *Lyria* sp. [8]; ?*Lyria* sp. [2]; *Acteonella* sp. cf. *borneensis* Nuttall & Leong [30]; *Acteonella laevis laevis* (J. de C. Sowerby) [1]; *Acteonella* sp. [4]; *Neocylindrites* sp. [2]; oliviform opisthobranch [1]; ?*Scaphander* sp. [1]; bullaeform opisthobranchs [2]; elongate opisthobranch [1]. **Cephalopods:** *Cimomia* cf. *sowerbyana* (d'Orbigny) [1]; *Brahmaites (Anabrahmaites) vishnu* (Forbes) [1]. **Corals:** *Cunnolites* sp. [42]; *Diploctenium* sp. [9]; *Aspidastraea* sp. [2]. **Decapod crustacean**: pagurid claw [1].

Bed 3 (upper part). Echinoids: *Hattopsis sphericus* Ali [3]; phymosomatid fragment [1]; *Conulus douvillei* (Cotteau & Gauthier) [1]; *Zuffardia morgani* (Cotteau & Gauthier) [1]; *Hemipneustes* sp. [3, fragments]. **Bivalves:** ?*Chlamys* sp. [1]; ?*Ctenoides* sp. [1]; Cardiidae [3]; ?*Fragum* sp. [2]. **Gastropods:** ?Umboniinae, gen. nov. [6]; ?*Rhabdoconcha* sp. [2]; *Campanile* sp. [1]; ?Cerithiidae indet. [3]; ?'*Ampullina* aff. *splendida*' (Deshayes) [1]; ?*Tylostoma incerta* (Forbes) [4]; ?Naticidae sp. [2]; Cypreidae spp. [3]; *Lyria* sp. [2]; elongate, fusiform genus [1].

Bed 4. Echinoids: *Glyphopneustes hattaensis* Ali [1]; *Hattopsis sphericus* Ali [15]; *Hemipneustes arabicus* Ali [3]. **Bivalves:** *Neithea* sp. [1]; *Durania* form B [1]; ?*Pycnodonte uncinella* (Leymerie) [7]; cf. *Fragum* sp. [3]. **Gastropods:** ?*Angaria* sp. [1]; ?Trochacea, euomphalid gen. nov. [3]; ?Umboniinae, gen. nov. [4]; Turritellidae [1]; ?Cerithiidae, sp. [2]; Cypraeidae, sp. [1]; *Caricella* sp. [2]. **Cephalopod:** *Cimonia* aff. *sowerbyana* (d'Orbigny) [1]. **Decapod crustacean**: small spinose pincers [2].

Bed 4 (top). Echinoids: *Salenia nutrix* Peron & Gauthier [2]; *Hattopsis sphericus* Ali [29]; *Noetlingaster emiratescus* Ali [1]; *Noetlingaster* sp. [1, fragment]; *Phymechinus perplexus* sp. nov. [2]; '*Globator*' *bleicheri* (Thomas & Gauthier) [15]; *Faujasia eccentripora* Lees [2]; *Hemipneustes persicus* Cotteau & Gauthier [1, fragment]. **Bivalves:** ?'*Mytilus*' *nitens* Forbes [1, bivalved]; '*Modiolus*' aff. *typicus* Forbes [2, bivalved]; *Endocostea (Selenoceramus) semaili* sp. nov. [2]; *Neithea* sp. [6]; ?*Pycnodonte uncinella* (Leymerie) [16]; *Scabrotrigonia* sp. [5, 1 bivalved]; *Gyropleura* sp. [4]; ?*Tellinella* sp. [1, bivalved]; 'Quenstedtiidae', gen. nov. [1]; Clavagellidae, gen. nov. [3]. **Gastropods:** ?Umboniinae, gen. nov. [27]; Turritellidae [1]; ?*Rhabdoconcha* sp. [2]; Cerithiidae [1]; Strombidae, gen. nov. [3]; Buccinacea sp. [1]; *Lyria* sp. [2]; ?*Volutomorpha* sp. [2]; Volutidae, cf. *Melo* [1]; ?Cancellariidae [1]; ?Neogastropods indet. [5]. **Cephalopod:** *Cimonia* cf. *sowerbyana* (d'Orbigny) [1]. **Corals:** *Cunnolites* sp. [4].

Collected in scree or from slipped blocks. Echinoids: *Orthopsis miliaris* (d'Archiac) [4]; *Salenia nutrix* Peron & Gauthier [1]; *Noetlingaster* sp. [1, fragment]; '*Globator*' *bleicheri* (Thomas & Gauthier) [2]; *Faujasia eccentripora* Lees [6]; *Petalobrissus* sp. [2]; *Hemipneustes compressus* Noetling [1]; *Hemipneustes* sp. [2, fragments]. **Bivalves:** *Cucullaea* sp. A [2, 1 bivalved]; *Neithea regularis* (Schlotheim) [1]; *Pycnodonte vesicularis* (Lamarck) [2]; ?*Pycnodonte uncinella* (Leymerie) [2]; *Agerostrea ungulata* (Schlotheim) [3]; *Scabrotrigonia* sp. [14]; *Glabrobournonia arabica* Morris & Skelton, sp. nov. [1]; Radiolitidae [1]; Tancrediidae, cf. *Tatella*, sp. nov. [1, bivalved]. **Gastropods:** '*Tectus*' sp. [1]; Turbinidae [1];

?Umboniinae, gen. nov. [1]; ?Turritellidae indet. [1]; '*Ampullina* aff. *splendida*' (Deshayes) [2]; *Tylostoma incerta* (Forbes) [2]; ?Naticidae sp. [1]; ?*Cimolithium* sp. [1]; ?Aporrhaidae sp. [2]; *Lyria* sp. [3]; *Acteonella* sp. cf. *borneensis* Nuttall & Leong [8]; opisthobranch [1]. **Corals:** *Cunnolites* sp. [66]; *Diploctenium* sp. [1]. **Ammonites:** *Brahmaites (Anabrahmaites) vishnu* (Forbes) [1].

Bed 6. Echinoids: *Coenholectypus inflatus* (Cotteau & Gauthier) [8]; '*Globator*' *bleicheri* (Thomas & Gauthier) [1]; *Hemipneustes persicus* Cotteau & Gauthier [2]; *Hemiaster hattaensis* Ali [3].

Rebel Rawdah, Section 2

Bed 4: 60–120 cm above basal conglomerate. Echinoids: *Goniopygus arabicus* sp. nov. [1]; *Plistophyma asiaticum* Gauthier [1]; *Echinotiara perebaskinei* Lambert [6]; *Faujasia eccentripora* Lees [14]; *Petalobrissus rawdahensis* sp. nov. [3]. **Bivalve:** *Durania* [1]. **Gastropod:** ?'*Ampullina* aff. *splendida*' (Deshayes) [2]. **Decapod crustacean:** limb segments [4].

Bed 5. Echinoids: *Faujasia eccentripora* Lees [2].

Beds 6–8. Echinoids: *Salenia nutrix* Peron & Gauthier [10]; *Goniopygus arabicus* sp. nov. [6]; *Codiopsis lehmanni* sp. nov. [1]; *Phymechinus perplexus* sp. nov. [6]; ?*Phymechinus* sp. [1]; *Echinotiara perebaskinei* Lambert [58]; *Coenholectypus inflatus* (Cotteau & Gauthier) [1]; '*Globator*' *bleicheri* (Thomas & Gauthier) [1]; *Faujasia eccentripora* Lees [92]; *Petalobrissus rawdahensis* sp. nov. [4]; *Petalobrissus* cf. *setifensis* (Cotteau) [9]; *Hemipneustes arabicus* Ali [1]. **Bivalve:** ?*Ctenoides* sp. [1]; *Durania* form B [4]. **Coral:** *Cunnolites* sp. [1]. **Decapod crustacean:** limb and claw segments [4].

Bed 10. Echinoids: *Goniopygus arabicus* sp. nov. [1]; *Glyphopneustes hattaensis* Ali [2]; *Faujasia eccentripora* Lees [1]; *Petalobrissus* sp. [2]. **Bivalves:** *Durania* cf. *apula* (Parona) [1]. **Gastropod:** Strombacea [1].

Bed 11: *Cucullaea* bed immediately overlying orange-weathering band. Echinoids: *Noetlingaster paucituberculatus* (Noetling) [1, fragment].

Bed 11 (middle, *ca.* 1 m above orange-weathering band). Echinoids: *Goniopygus arabicus* sp. nov. [1]; *Faujasia eccentripora* Lees [6]; *Petalobrissus* sp. [1]; *Nucleopygus magnus* sp. nov. [4]; *Stigmatopygus pulchellus* sp. nov. [2]; *Hemipneustes arabicus* Ali [4]. **Gastropods:** ?Umboniinae, gen. nov. [1]; *Campanile* sp. [1]; *Pyrazus* sp. [1]; Strombidae, gen. nov. [1]; Volutidae sp. [3].

Bed 11: 2.5 m above base. Echinoids: *Echinotiara perebaskinei* Lambert [18]; *Coenholectypus* cf. *baluchistanensis* (Noetling) [1]; *Faujasia eccentripora* Lees [49]; *Petalobrissus* sp. [40]. **Gastropod:** '*Ampullina* aff. *splendida*' *(Deshayes) [1].* Corals: *Cunnolites* sp. [3]; massive meandroid colony [1].

Bed 11 (unspecified). Echinoids: *Salenia nutrix* Peron & Gauthier [2]; *Glyphopneustes emiratensis* Ali [5]; *Hattopsis sphericus* Ali [2]; *Noetlingaster paucituberculatus* (Noetling) [4]; *Phymechinus? perplexus* sp. nov. [1]; *Echinotiara perebaskinei* Lambert [3]; *Coenholectypus* cf. *baluchistanensis* (Noetling) [8]; '*Globator*' *bleicheri* (Thomas & Gauthier) [10]; *Faujasia eccentripora* Lees [46]; *Zuffardia morgani* (Cotteau & Gauthier) [41]; *Petalobrissus rawdahensis* sp. nov. [247]; *Petalobrissus* cf. *setifensis* (Cotteau) [124]. **Bivalves:** '*Modiolus*' aff. *typicus* Forbes [1, bivalved]; *Cucullaea* sp. A [8, bivalved]; *Pholadomya* sp. C. cf. *P. connectans* Forbes [22, bivalved]. **Coral:** *Cunnolites* sp. [1].

Bed 13. Echinoids: *Salenia nutrix* Peron & Gauthier [2]; *Glyphopneustes hattaensis* Ali [1]; '*Globator*' *bleicheri* (Thomas & Gauthier) [1]; *Petalobrissus rawdahensis* sp. nov. [230]; *Petalobrissus* cf. *setifensis* (Cotteau) [4]; *Nucleopygus magnus* sp. nov. [3]. **Bivalves:** '*Modiolus*' aff. *typicus* Forbes [1, bivalved]; *Dictyoptychus morgani* (Douvillé) [common]; ?*Biradiolites* aff. *baylei* Toucas [1]; ?*Fragum* sp. [1]; ?Clavagellidae indet. [1]. **Gastropods:** ?Umboniinae, gen. nov. [6]; Turritellidae, sp. [1]; ?*Rhabdoconcha* sp. [1]; ?*Cimolithium* sp. [2]; '*Ampullina* aff. *splendida*' (Deshayes) [4]; Cypraeidae, sp. [1]; cf. ?Columbellidae [2]; ?Neogastropod indet. [1]. **Corals:** *Cunnolites* sp. [15]; *Diploctenium* sp. [2]; *Aspidastraea* sp. [1].

Bed 14. Echinoids: *Noetlingaster paucituberculatus* (Noetling) [5 plus fragments]; *Phymechinus* ? sp. [1]; '*Globator*' *bleicheri* (Thomas & Gauthier) [7]; *Conulus douvillei* (Cotteau & Gauthier) [1]; *Faujasia eccentripora* Lees [7]; *Pygurostoma morgani* Cotteau & Gauthier [3]; *Arnaudaster cylindriformis* sp. nov. [4]; *Petalobrissus rawdahensis* sp. nov. [17]; *Petalobrissus* cf. *setifensis* (Cotteau) [15]; *Petalobrissus linguiformis* (Peron & Gauthier) [4]; *?Stigmatopygus pulchellus* sp. nov. [6]; *Hemipneustes arabicus* Ali [1]; *H. compressus* Noetling [2]. **Gastropods:** *Campanile* sp. [2]; ?*Campanile* sp. [1]; '*Ampullina* aff. *splendida*' (Deshayes) [2]; ?*Pseudocassis* sp. [1]; Strombidae, gen. nov. [2]; Fasciculariidae, sp. [1]; ?Volutidae indet. [1]. **Corals:** *Aspidastraea* sp. [1].

Bed 15. Echinoids: *Conulus douvillei* (Cotteau & Gauthier) [2]; *Petalobrissus rawdahensis* sp. nov. [25]; *Hemipneustes compressus* Noetling [2]. **Bivalves:** ?*Granocardium* sp. [3]; rudist [1]. **Gastropods:** *Pyrazus* sp. [2]; Cerithiidae [1]; ?Naticidae, sp. [1]; Strombidae gen. nov. [3]. **Corals:** *Cunnolites* sp. [21]; *Aspidastraea* sp. [9]; massive meandroid colony [1].

Beds 16–19. Bivalve: '*Modiolus*' aff. *typicus* Forbes [1, bivalved]. **Corals:** *Cunnolites* sp. [2]; *Aspidastraea* sp. [2].

Bed 16. Echinoids: '*Globator*' *bleicherei* (Thomas & Gauthier) [3]; *Faujasia eccentripora* Lees [3]; *Petalobrissus rawdahensis* sp. nov. [5]. **Bivalves:** *Neithea regularis* (Schlotheim) [1] *Durania* spp. [several]; Veneridae [2]. **Gastropods:** ?*Rhabdoconcha* sp. [1]; ?Cerithiidae [1]; '*Ampullina*' aff. *splendida* (Deshayes) [3]; Strombidae [1]; Cypraeidae [1].

Bed 18. Echinoid: *Pygurostoma morgani* Cotteau & Gauthier [1]. Bivalves: ?*Granocardium* sp. [1]. **Gastropods:** ?Umboniinae gen. nov. [1]; ?*Cimolithium* sp. [2]; Strombidae, gen. nov. [1].

Bed 19. Echinoids: *Noetlingaster paucituberculatus* (Noetling) [4]; *Coenholectypus inflatus* (Cotteau & Gauthier) [1]; '*Globator*' *bleicheri* (Thomas & Gauthier) [8]; *Vologesia rawdahensis* Ali [1]; *Zuffardia morgani* (Cotteau & Gauthier) [5]; *Faujasia eccentripora* Lees [19]; *Arnaudaster cylindriformis* sp. nov. [1]; *Petalobrissus rawdahensis* sp. nov. [73]; *Petalobrissus* cf. *setifensis* (Cotteau) [23]; *Petalobrissus linguiformis* (Peron & Gauthier) [5]; *?Stigmatopygus pulchellus* sp. nov. [1]; *Pygurostoma morgani* Cotteau & Gauthier [2]; *Hemipneustes compressus* Noetling [1]; *Hemipneustes persicus* (Cotteau & Gauthier) [1]. **Bivalves:** ?*Granocardium* sp. [2]; *Isognomon* sp. [1]; ?Lucinidae indet. [1]; *Dictyoptychus morgani* (Douvillé) [1]; Veneridae, gen. indet. [1]. **Gastropods:** ?Umboniinae, gen. nov. [9]; ?*Rhabdoconcha* sp. [1]; ?Cerithiidae [5]; *Campanile* sp. [4]; '*Ampullina* aff. *splendida*' (Deshayes) [3]; *Tylostoma incerta* (Forbes) [2]; ?Naticidae [4]; Strombidae, gen. nov. [5]; Cypraeidae, sp. [1]; Fasciolariidae or Buccinidae [1]; *Canalicella* sp. [1]; Volutidae [3]; *Acteonella* sp. [1]. **Corals:** *Neocaeniopsis reussi* (Edwards & Haime) [1]; *Astrogyra edwardsi* (Reuss) [1]; cerioid colonies [2]; *Cunnolites* sp. [17]; *Diploctenium* sp. [1]; *Aspidastraea* sp. [8]; massive meandrine colonies [5].

Bed 20. Echinoids: '*Globator*' *bleicheri* (Thomas & Gauthier) [2]; *Faujasia eccentripora* Lees [2]; *Petalobrissus linguiformis* (Peron & Gauthier) [1]; *Petalobrissus* sp. [1]; *Hemipneustes compressus* Noetling [1]; *Hemipneustes persicus* (Cotteau & Gauthier) [1]. **Gastropods:** ?*Angaria* sp. [1]; ?Umboniinae gen. nov. [2]; '*Ampullina* aff. *splendida*' (Deshayes) [3]; Strombidae, gen. nov. [5].

Bed 21 (base). Echinoids: *Noetlingaster paucituberculatus* (Noetling) [1]; '*Globator*' *bleicheri* (Thomas & Gauthier) [1]; *Conulus douvillei* (Cotteau & Gauthier) [2]; *Faujasia eccentripora* Lees [22]; *Zuffardia morgani* (Cotteau & Gauthier) [5]; *Pygurostoma morgani* Cotteau & Gauthier [7]; *Arnaudaster cylindriformis* sp. nov [1]; *Petalobrissus rawdahensis* sp. nov. [45]; *Petalobrissus* cf. *setifensis* (Cotteau) [44]; *Petalobrissus linguiformis* (Peron & Gauthier) [4]; *?Stigmatopygus pulchellus* sp. nov. [7]; *Hemip*

neustes compressus Noetling [16]; *Hemipneustes persicus* (Cotteau & Gauthier) [22]. **Bivalves:** *Barbatia* cf. *morgani* (Douvillé) [3, bivalved]; *Pycnodonte vesicularis* (Lamarck) [1]; heterodont indet. [1]. **Gastropods:** *Campanile* sp. [1]; '*Ampullina* aff. *splendida*' (Deshayes) [1]; Naticidae [2]; *Tylostoma incerta* (Forbes) [1]; Strombidae, gen. nov. [1]; ?Fasciolariidae [1]; bullaeform opisthobranch [1]. **Ammonite:** *Desmophyllites diphylloides* (Forbes) [1].

Bed 21 (middle). **Gastropods:** '*Ampullina* aff. *splendida*' (Deshayes) [4]; Strombidae, gen. nov. [3]; Strombidae, sp. [1]; ?*Hercorhynchus* sp. [1]; ?Buccinacea, sp. [1]; neogastropod, gen. A [2]; neogastropod, gen. B [1].

Bed 22. Echinoids: '*Globator*' *bleicheri* (Thomas & Gauthier) [1]; *Faujasia eccentripora* Lees [3]; *Petalobrissus rawdahensis* sp. nov. [13]; *Hemipneustes compressus* Noetling [1]. **Gastropods:** '*Ampullina* aff. *splendida*' (Deshayes) [2]; ?Buccinacea [1].

Bed 23 (base). **Echinoids:** *Petalobrissus* sp. [1]. **Gastropods:** *Pyrazus* sp. [1]; Naticidae [1].

Beds 23–25. Echinoids: *Petalobrissus* sp. [5]; *Faujasia eccentripora* Lees [1]. **Bivalves:** ?*Biradiolites* aff. *baylei* Toucas [2].

Bed 25. Echinoids: *Noetlingaster paucituberculatus* (Noetling) [4]; *Faujasia eccentripora* Lees [3]; *Zuffardia morgani* (Cotteau & Gauthier) [1]; *Petalobrissus* sp. [11]. **Bivalve:** ?Lucinidae indet. [1].

Bed 26. Echinoids: *Coenholectypus inflatus* (Cotteau & Gauthier) [1]; *Arnaudaster cylindriformis* sp. nov. [1]; *Pygurostoma morgani* Cotteau & Gauthier [2]; *Petalobrissus rawdahensis* sp. nov. [5]; *Petalobrissus* cf. *setifensis* (Cotteau) [3]; *Hemipneustes compressus* Noetling [2]; *Hemipneustes* sp. fragment [1]. **Bivalve:** *Neithea* sp. [1].

Bed 27. Echinoids: *Hemipneustes compressus* Noetling [2].

Bed 28. Bivalves: Indet. small rudists.

Loose: a little below beds 21/22 and probably derived from them. Echinoids: *Hemipneustes arabicus* Ali [1].

Loose: scree from level of bed 11 (derived from beds 13–15 mostly). Echinoids: *Coenholectypus inflatus* (Cotteau & Gauthier) [1]; *Conulus douvillei* (Cotteau & Gauthier) [1]; *Faujasia eccentripora* Lees [14]; *Zuffardia morgani* (Cotteau & Gauthier) [3]; *Petalobrissus linguiformis* (Peron & Gauthier) [6]; *Petalobrissus* sp. [2].

Loose, scree. Echinoids: *Glyphopneustes hattaensis* Ali [2]; *Echinotiara perebaskinei* Lambert [2]; *Coenholectypus inflatus* (Cotteau & Gauthier) [1]; '*Globator*' *bleicheri* (Thomas & Gauthier) [4]; *Faujasia eccentripora* Lees [32]; *Zuffardia morgani* (Cotteau & Gauthier) [11]; *Arnaudaster cylindriformis* sp. nov. [1]; *Pygurostoma morgani* Cotteau & Gauthier [1]; *Petalobrissus* sp. [62]; *Nucleopygus magnus* sp. nov. [3]; *Hemipneustes persicus* (Cotteau & Gauthier) [4]; *Hemiaster hattaensis* Ali [1]. **Bivalves:** '*Modiolus*' aff. *typicus* Forbes [1, bivalved]; *Spondylus* sp. C [1]; *Amphidonte pyrenaicum* (Leymerie) [1]; *Dictyoptychus morgani* (Douvillé) [1]; *Radiolites* sp. [1]; ?*Biradiolites* aff. *baylei* Toucas [2]. **Gastropods:** ?Umboniinae, gen. nov. [3]; *Pyrazus* sp. [1]; *Campanile* sp. [1]; '*Ampullina* aff. *splendida*' (Deshayes) [1]; ?*Perrisoptera* sp. [1]; *Caricella* sp. [2]; *Acteonella* sp. [1]; *Acteonella* cf. *caucasica* Zekeli [1]. **Corals:** *Cunnolites* sp. [12]; *Aspidastraea* sp. [1].

Loose, lower part of section (from beds 1–11). Echinoids: *Salenia nutrix* Peron & Gauthier [3]; *Goniopygus arabicus* sp. nov. [4]; *Glyphopneustes hattaensis* Ali [4]; *Hattopsis sphericus* Ali [1]; *Noetlingaster paucituberculatus* Noetling [1]; *Phymechinus? perplexus* sp. nov. [4]; *Echinotiara perebaskinei* Lambert [15]; *Coenholectypus baluchistanensis* Noetling [5]; '*Globator*' *bleicheri* (Thomas & Gauthier) [9]; *Faujasia eccentripora* Lees [80]; *Zuffardia morgani* (Cotteau & Gauthier) [29]; *Petalobrissus* spp. [136]. **Asteroid:** marginal [1]. **Brachiopod:** terebatulid, gen. nov. [1].

Loose, mid-section. Echinoids: *Salenia* sp. [1]; *Zuffardia morgani* (Cotteau & Gauthier) [6]; ?*Stigmatopygus pulchellus* sp. nov. [1]. **Corals:** *Cunnolites* sp. [2]; *Aspidastraea* sp. [1].

Jebel Rawdah, Section 3a

Bed 2. Echinoids: *Goniopygus arabicus* sp. nov. [2]. **Bivalve:** *Durania* sp. [1]. **Gastropod:** *Acteonella* sp. [1].

Bed 4. Echinoid: *Echinotiara perebaskinei* Lambert [1]. **Bivalves:** *Pycnodonte vesicularis* (Lamarck) [1]; *Amphidonte pyrenaicum* (Leymerie) [2, bivalved].

Bed 5. Bivalves: '*Modiolus*' aff. *typicus* Forbes [1, bivalved]; ?'*Mytilus*' *nitens* Forbes [1, bivalved]; *Barbatia* sp. B [3]; *Neithea regularis* (Schlotheim) [3]; *Amphidonte pyrenaicum* (Leymerie) [3]; *Agerostrea ungulata* (Schlotheim) [9]; Eligmidae [5, bivalved]; *Crassitellites* sp. [5].

Bed 7 (near top). Echinoid: '*Globator*' *bleicheri* (Thomas & Gauthier) [1]. **Bivalves:** *Pycnodonte vesicularis* (Lamarck) [1]; *Agerostrea ungulata* (Schlotheim) [1, bivalved]; ?*Clavagella* sp. [tubes]. **Gastropods:** Naticidae, indet. [2].

Loose, derived from lower beds. Bivalves: *Plicatula hirsuta* Coquand [1]; ?*Pycnodonte uncinella* (Leymerie) [2, bivalved]. **Gastropod:** Turritellidae [1].

Jebel Rawdah, Section 3b

Bed 2 (lower part). Echinoids: *Orthopsis miliaris* (d'Archiac) [1]; *Glyphopneustes hattaensis* Ali [1]; *Circopeltis emiratus* sp. nov. [1]; *Faujasia eccentripora* Lees [3]. **Coral:** *Cunnolites* sp. [1]. **Decapod crustacean:** *Callianassa* (limb segment) [1].

Bed 2 (upper part). Echinoids: *Salenia nutrix* Peron & Gauthier [1]; *Glyphopneustes hattaensis* Ali [1]; '*Globator*' *bleicheri* (Thomas & Gauthier) [11]; *Petalobrissus rawdahensis* sp. nov [19]; *Petalobrissus* cf. *setifensis* (Cotteau) [4]; *Nucleopygus magnus* sp. nov. [3]. **Coral:** ?*Diploctenium* sp. [1].

Bed 3. Echinoid: *Echinotiara perebaskinei* Lambert [1]. **Bivalve:** *Pycnodonte vesicularis* (Lamarck) [1].

Bed 4. Corals: large meandrine colonies [2]; placoid colony [1].

Bed 5. Echinoids: *Heterodiadema buhaysensis* sp. nov. [1]; *Glyphopneustes hattaensis* Ali [1]; *Coenholectypus inflatus* (Cotteau & Gauthier) [3]; '*Globator*' *bleicheri* (Thomas & Gauthier) [1]; *Hemipneustes* sp. [1]; *Hemiaster hattaensis* Ali [1]. **Bivalve:** *Pycnodonte vesicularis* (Lamarck) [1].

Bed 5/6. Echinoids: '*Globator*' *bleicheri* (Thomas & Gauthier) [8]; *Hemipneustes persicus* Cotteau & Gauthier [1]; *Mecaster victoris* Lambert [47].

Bed 6. Echinoid: *Circopeltis emiratus* sp. nov. [1]. **Bivalve:** Eligmidae [1]. **Gastropod:** *Tylostoma incerta* (Forbes) [1].

Bed 7. Echinoids: *Coenholectypus inflatus* (Cotteau & Gauthier) [1]; *Hemipneustes persicus* Cotteau & Gauthier [1]. **Bivalves:** *Barbatia* sp. B [1, bivalved)]; '*Modiolus*' aff. *typicus* Forbes [2, bivalved].

Bed 8. Echinoids: *Orthopsis miliaris* (d'Archiac) [1]; *Actinophyma spectabile* Cotteau & Gauthier [1]; *Coenholectypus* sp. [1]; *Vologesia rawdahensis* Ali [1]; *Faujasia eccentripora* Lees [1]; *Mecaster* sp. [6]. **Coral:** *Cunnolites* sp. [1]. **Decapod crustacean:** pincer [1].

Bed 9. Echinoids: *Orthopsis miliaris* (d'Archiac) [7]; *Noetlingaster* sp. [1, fragment]; *Actinophyma spectabile* Cotteau & Gauthier [1]; '*Globator*' *bleicheri* (Thomas & Gauthier) [1]; *Faujasia eccentripora* Lees [3]; *Hemipneustes compressus* Noetling [2]; *Hemiaster* sp. cf. *H. hattaensis* Ali [1]; *Mecaster victoris* Lambert [1]; *Proraster geayi* Cottreau [2]. **Bivalves:** *Cucullaea* sp. A [4]; *Scabrotrigonia* sp. [8, 1 bivalved]; ?Tancrediidae, sp. nov. [1]. **Gastropods:** *Acteonella* sp. cf. *borneensis* Nuttall & Leong [1]; *Acteonella sp. [2]*. **Corals:** *Cunnolites* sp. [8]; *Diploctenium* sp. [1]; thamnasteroid colony [1].

Bed 11. Echinoids: *Coenholectypus inflatus* (Cotteau & Gauthier) [1]; '*Globator*' *bleicheri* (Thomas & Gauthier) [1]; *Arnaudaster cylindriformis* sp. nov. [1]. **Bivalves:** *Barbatia* sp. B [2]; '*Modiolus*' aff. *typicus* Forbes [1, bivalved]; ?*Pycnodonte uncinella* (Leymerie) [3, bivalved]; *Amphidonte pyrenaicum* (Leymerie) [2, 1 bivalved];

Agerostrea ungulata (Schlotheim) [21]; *Scabrotrigonia* sp. [7, 1 bivalved]. **Gastropod:** *Caricella* sp. [1].

Loose. Echinoids: *Prionocidaris morgani* (Gauthier) [1]; *Orthopsis miliaris* (d'Archiac) [3]; *Coenholectypus inflatus* (Cotteau & Gauthier) [6]; *'Globator' bleicheri* (Thomas & Gauthier) [3]; *Conulus douvillei* (Cotteau & Gauthier) [4]; *Hemipneustes compressus* Noetling [1].

Loose near top of section. Echinoids: *Arnaudaster cylindriformis* sp. nov. [1]; *?Linthia sudanensis* (Bather) [1].

Jebel Rawdah, Section 4

Bed 1. Bivalves: *Dictyoptychus morgani* (Douvillé) [1]; *Praeradiolites* cf. *subtoucasi* Toucas [4]; *Pseudosabinia* aff. *klinghardti* Boehm [3]; *Pseudosabinia* sp. [1].

Bed 1/2. Echinoids: *Phymosoma hexaoporum* Lambert [1]; *'Globator' bleicheri* (Thomas & Gauthier) [6]. **Bivalves:** *Scabrotrigonia* sp. [2]; *Glabrobournonia arabica* Morris & Skelton, sp. nov. [21].

Bed 2 (mostly near top). Echinoids: *Echinotiara perebaskinei* Lambert [1]; *Coenholectypus* sp. indet. [1]; *'Globator' bleicheri* (Thomas & Gauthier) [3]; *Faujasia eccentripora* Lees [1]; *Zuffardia morgani* (Cotteau & Gauthier) [2]; *Petalobrissus* cf. *setifensis* (Peron & Gauthier) [1]; *Hemiaster hattaensis* Ali [1]. **Bivalves:** *Neithea regularis* (Schlotheim) [1]; *Pycnodonte vesicularis* (Lamarck) [1]; *?Pycnodonte uncinella* (Leymerie) [3, 1 bivalved]; *Amphidonte pyrenaicum* (Leymerie) [1]; *Scabrotrigonia* sp. [1]. **Gastropod:** *Acteonella* sp. cf. *borneensis* Nuttall & Leong [1].

Bed 4. Echinoids: *Glyphopneustes hattaensis* Ali [1]; *Circopeltis emiratus* sp. nov. [1]; *'Globator' bleicheri* (Thomas & Gauthier) [4]; *Faujasia eccentripora* Lees [2]; *Petalobrissus* sp. [1]. **Corals:** *Cunnolites* sp. [2]; *Aspidastraea* sp. [1].

Bed 5. Echinoid: *'Globator' bleicheri* (Thomas & Gauthier) [1].

Bed 8. Echinoids: *Orthopsis miliaris* (d'Archiac) [1]; *Echinotiara perebaskinei* Lambert [1]; *'Globator' bleicheri* (Thomas & Gauthier) [3]; *Conulus douvillei* (Cotteau & Gauthier) [1]; *Petalobrissus* cf. *setifensis* (Cotteau) [3].

Bed 9. Bivalves: *Amphidonte pyrenaicum* (Leymerie) [1]; *Scabrotrigonia* sp. [common].

Bed 10. Echinoids: *Orthopsis miliaris* (d'Archiac) [6]; *Salenia nutrix* Peron & Gauthier [1]; *'Globator' bleicheri* (Thomas & Gauthier) [10]. **Bivalve:** *Dictyoptychus* sp. [1]. **Corals:** cerioid colony [1]; placoid colony [1].

Bed 12. Echinoids: *Coenholectypus* sp. [1]; *'Globator' bleicheri* (Thomas & Gauthier) [5]; *Nucleopygus magnus* sp. nov. [1]. **Sponge:** chaetetid [1].

Bed 13. Echinoids: *Noetlingaster emiratescus* Ali [2]; *Coenholectypus inflatus* (Cotteau & Gauthier) [1]; *'Globator' bleicheri* (Thomas & Gauthier) [3]; *Conulus douvillei* (Cotteau & Gauthier) [1]; *Hemiaster hattaensis* Ali [1].

Bed 15. Echinoids: *Orthopsis miliaris* (d'Archiac) [1]; *'Globator' beleicheri* (Thomas & Gauthier) [1]. **Coral:** *Actinacis* sp. [1].

Bed 18. Echinoid: *Coenholectypus* sp. [1].

Bed 19. Echinoids: *Coenholectypus inflatus* (Cotteau & Gauthier) [1]; *'Globator' bleicheri* (Thomas & Gauthier) [1]; *Pygurostoma morgani* Cotteau & Gauthier [1].

Bed 22/23. Echinoids: *Coenholectypus inflatus* (Cotteau & Gauthier) [1]; *Faujasia eccentripora* Lees [1].

30 cm below top of measured section. Echinoids: *Coenholectypus inflatus* (Cotteau & Gauthier) [1]. **Bivalve:** *Neithea regularis* (Schlotheim) [1].

Loose, a little below the top of the section. Echinoids: *Hemipneustes arabicus* Ali [1].

Loose at level of bed 3. Echinoid: *Petalobrissus linguiformis* (Peron & Gauthier) [1].

Loose. Echinoids: *Orthopsis miliaris* (d'Archiac) [1]; *Conulus douvillei* (Cotteau & Gauthier) [1]; *Petalobrissus* sp. [1]. **Bivalves:** *Amphidonte pyrenaicum* (Leymerie) [2].

Jebel Faiyah, Section 1a

Bed 6. Bivalves: *Hippurites* aff. *lapeirousei* Goldfuss [1 colony].

Bed 8. Bivalves: *Agerostrea ungulata* (Schlotheim) [2]; *?Pycnodonte uncinella* (Leymerie) [18]; *?Amphidonte* cf. *pyrenaicum* (Leymerie) [1].

Jebel Faiyah, Section 1b

Bed 2 (lower part). Echinoids: *Hattopsis paucituberculatus* sp. nov. [6]. **Corals:** *Polytremacis* sp. [1]; *Astraraea* sp. [1]; *Hydnophoraraea* sp. [1]. **Sponge:** chaetetid [1].

Bed 2 (upper part). Echinoids: cidarid [1]; *Orthopsis miliaris* (d'Archiac) [1]; *Salenia nutrix* Peron & Gauthier [2]; *Glyphopneustes hattaensis* Ali [1]; *Hattopsis paucituberculatus* sp. nov. [1]; *'Globator' bleicheri* (Thomas & Gauthier) [1]; *Nucleopygus magnus* sp. nov. [1]; *Hemiaster* sp. cf. *H. hattaensis* Ali [1]. **Bivalves:** *Hippurites* cf. *lapeirousei* Goldfuss [1 colony]; *Hippurites* aff. *cornucopiae* Defrance [1]; *Dictyoptychus morgani* (Douvillé) [2]; *Biradiolites* aff. *baylei* Toucas [1]; *Durania* cf. *gaensis* (Dacqué) [1]. **Decapod crustacean:** pincers [2].

Bed 4. Bivalves: *Hippurites* aff. *lapeirousei* Goldfuss [2]. **Corals:** *Polytremacis* sp. [1]; *Hydnophoraraea* sp. [1]; *Paraplacocoenia orbignyana* (Reuss) [1]; *Moltkia isis* Sreenstrup [1].

Bed 5. Echinoids: *Glyphopneustes hattaensis* Ali [2].

Bed 6. Echinoid: cidarid spine [1]. **Coral:** *Moltkia isis* Sreenstrup [1].

Bed 7. Echinoids: cidarid spine [1]; *Mimiosalenia quinquetuberculata* sp. nov. [21]; *Hattopsis sphericus* Ali [1]; *'Globator' bleicheri* (Thomas & Gauthier) [36].

Bed 8. Coral: *Cunnolites* sp. [1].

Loose (derived from beds 2–5). Echinoids: *Hattopsis paucituberculatus* sp. nov. [5]. **Bivalves:** *Spondylus* sp. C [2]. **Nautiloid:** *Deltoidonautilus salisfilius* sp. nov. [1]. **Corals:** *Polytremacis* sp. [5]; *Cunnolites* sp. [1]; *Paraplacocoenia orbignyana* (Reuss) [1]; *Hydnophoraraea* sp. [5]; turbinate solitary [1]; cerioid colonies (6 genera) [14]; flabellate solitary [1]; phaceloid colony [1]. **Branching algae** [1]. **Sponge:** chaetetid [1]. **Decapod crustacean:** crab carapace [1].

Jebel Faiyah – southern nose of Jebel (bed numbers as in section 1a)

Bed 8. Echinoids: *Salenia* sp. [1]; *Glyphopneustes hattaensis* Ali [8]; *Hattopsis sphericus* Ali [8]; *'Globator' bleicheri* (Thomas & Gauthier) [2]; *Pygurostoma morgani* Cotteau & Gauthier [1]. **Corals:** *Cunnolites* sp. [2].

Loose. Echinoids: *Hattopsis sphericus* Ali [1]. **Bivalves:** *?Barbatia* sp. A. cf. *B. morgani* (Douvillé) [1, bivalved]; *Neithea regularis* (Schlotheim) [7]; *?Pycnodonte uncinella* (Leymerie) [18]; *?Plagioptychus* sp. [1]; *Glabrobournonia arabica* Morris & Skelton, sp. nov. [1]; *Hippurites ?cornucopiae* Defrance [11]; *Dictyoptychus morgani* (Douvillé) [3]. **Gastropod:** *Tylostoma incerta* (Forbes) [1]. **Corals:** *Moltkia isis* Streenstrup [1]; *Cunnolites* sp. [3]; *Hydnophoraraea* sp. [2]; *Paraplacocoenia orbignyana* (Reuss) [1]; cerioid colonies (3 genera) [4]; phlacoid colony [1]; thamnasteroid colony [1].

Jebel Faiyah, Section 2

Basal 1 m shell bed. Bivalves: *Glabrobournonia arabica* Morris & Skelton, sp. nov. [3]. **Nautiloids:** *Cimonia* cf. *sowerbyana* (d'Orbigny) [1]; *Deltoidonautilus salisfilius* sp. nov. [2].

Jebel Bu Milh, Section 1

Bed 1. Bivalves: *Pseudosabinia* aff. *klinghardti* (Boehm) [4]; *Durania* cf. *gaensis* (Dacqué).

Bed 3. Bivalves: *'Modiolus'* aff. *typicus* Forbes [1, bivalved]; *Lyrio-*

chlamys ternatus (Münster) [2]; *Neithea regularis* (Schlotheim) [1]; ?*Plagioptychus* sp. [4, lids]; *Dictyoptychus morgani* (Douvillé) [1, juvenile]; *Radiolites* sp. [3]; *Eodictyoptychus* aff. *arumaensis* Skelton & El-Asa'ad [2]. **Gastropods:** ?'*Angaria*'/*Liotia* sp. [1, fragment]; ?trochid [1]; *Discotectus* sp. [26]; *Strigosella* sp. cf. *striolata* (Stolizcka) [2]; *Euchelus ornatus* Stolizcka [3]; ?*Umbonium greyi* Lees [1]; '*Turritella*' sp. [1]; '*Turritella*' sp. 1 ?= *Nairiella multistriata* (Reuss) [4]; *Vermetus* sp. [2]; *Campanile curtum* Douvillé [1]; *Campanile persicum* Douvillé [2]; *Campanile* aff. *breve* Lees [1, fragment]; *Campanile morgani* Douvillé [1]; *Campanile* sp. [6, internal moulds]; *Campanile* cf. *ganesha* Noetling [4]; *Cimolithium* sp. nov. [2]; *Pyrazus* sp. [1]; *Paryphostoma morgani* Douvillé [1]; *Pugnellus* sp. [2]; *Ampullina* aff. *splendida* (Deshayes) [30+]; '*Euspira*' *lirata* J. de C. Sowerby [22]; '*Natica*' *pagoda* Forbes [2]; *Tylostoma incerta* (Forbes) [5]; *Confusiscala* sp. [1]; '*Cypraea*' *kayeii* Forbes [2]; *Hipponyx* sp. [1]; '*Fulguraria*' *multistriata* Stoliczka [1]; fasciolariid [1]; ?Rapanidae gen. indet. [1]; '*Murex*' sp. [1]; '*Trophon*' *oldhamianum* Stolizcka [1]; *Volutoderma elongata* Stolizcka [1]; *Volutolithes latisepta* Stoliczka [2]; *Caricella pyriformis* Forbes [2]; *Caricella* sp. [2]; '*Voluta*' sp. or spp. [3]; *Trochactaeon* sp. [1]; *Acteonella* cf. *caucasica* Zekeli [30+]; *Acteonella caucasica* Zekeli subsp. *grossouvrei* Cossmann [10]; *Acteonella laevis laevis* (J. de C. Sowerby) [4]; *Acteonella elongata* Kollmann [4]. **Corals:** *Aspidastraea* sp. [1]; *Hydnophoraraea* sp. [2].

Jebel Bu Milh, Section 2

Bed 4. Gastropods: *Acteonella* cf. *caucasica* Zekeli [74]; *Acteonella elongata* Kollmann [1]; *Acteonella laevis* (J. de C. Sowerby) [3]; *Acteonella* cf. *laevis zekelii* Kollmann [1]. **Bivalves:** *Lapeirousia* sp. [2].

Beds 7/8. Echinoids: *Petalobrissus* cf. *setifensis* (Cotteau) [1]. **Bivalves:** *Barbatia* sp. B [12, 4 bivalved]; *Cucullaea* sp. A [2, bivalved]; *Glycymeris* sp. [1]; '*Platyceramus*' sp. [1]; *Lyriochlamys ternatus* (Münster) [1]; *Neithea regularis* (Schlotheim) [1]; *Spondylus* sp. [4, bivalved]; *Plicatula hirsuta* Coquand [5]; *Plagiostoma* sp. [2]; *Crassatellites* sp. [5]; *Eodictyoptychus* aff. *arumaensis* Skelton & El-Asa'ad [1]; *Biradiolites* aff. *baylei* Toucas [1]. **Gastropods:** *Calliomphalus* sp. [2]; ?*Calliomphalus* or *Helicanthus* sp. [1]; ?'*Angaria*' sp. [2]; Cyclostrematid/Liotid gen. nov. [1]; cf. '*Turbo*' *punctatus* Zekeli [1, fragment]; *Discotectus* sp. 1 [common]; *Discotectus* sp. 2 [common]; *Strigosella* sp. cf. *striolata* (Stolizcka) [common]; *Nerita* spp. [occurs]; '*Lissocheilus*' *persicus* (Douvillé) [4]; '*Turritella*' sp. 1 ?= *Nairiella multistriata* (Reuss) [7]; '*Turritella*' sp. cf. *morgani* Douvillé [1]; '*Turritella*' sp. 3 (?= *Roemeriella nerinea* Akopyan (*non* Römer)) [2]; *Campanile ?robustum* Douvillé [1]; *Campanile curtum* Douvillé [26]; *Campanile ?persicum* Douvillé [2]; *Campanile* aff. *breve* (Lees) [5]; *Campanile morgani* Douvillé [1]; *Cimolithium* sp. nov. [72]; *Semivertagus* cf. *arcotense* Stolizcka [1]; cf. *Pyrazella (Plicopyrazus)* [1]; *Pyrazus pyramidatus* Douvillé [1]; *Exechocirsus* sp. 1 [2]; *Exechocirsus* sp. 2 [1]; ?*Exechocirsus* sp. [2]; ?*Semivertagus* sp. cf. *arcotense* (Stolizka) [7]; *Hantkenia louristana* Douvillé [5]; Strombidae gen. nov. *giganteus* Noetling [6]; Strombidae gen. nov. *digitatus* Noetling [2]; '*Helicaulax*' sp. [4]; *Ampullina* aff. *splendida* (Deshayes) [100]; '*Euspira lirata*' (J. de C. Sowerby) [1]; ?*Tylostoma incerta* (Forbes) [12]; '*Confusiscala*' sp. cf. *turbinata* Forbes [5]; '*Calyptraea*' *elevata* Forbes [1]; *Thlacodes lamellosus* Stolizcka [1]; *Lathyrus* sp. [1]; *Lathyrus* sp. cf. '*Ornopsis*' *digressa* (Wade) [1]; ?*Bellifusus* sp. [1]; ?*Pseudoliva* sp. [2]; '*Voluta*' *citharina* Forbes [1]; *Volutoderma* sp. [2]; *Caricella pyriformis* Forbes [20+]; '*Voluta*' sp. [11]; '*Voluta*' sp. [21]; *Voluta cameleo* Forbes [1]; *Volutoderma* sp. [1]; *Lyria crassicostata* Dujardin [2]; ?*Naronia eximia* Stolizcka [1]; *Acteonella caucasica* Zekeli *grossouvrei* Cossmann [46]; *Acteonella caucasica caucasica* Zekeli [31]; *Acteonella caucasica* Zekeli subsp. nov. [1]; *Acteonella laevis laevis* (J. de C. Sowerby) [3]; ?*Acteonella laevis* J. de C. Sowerby *zekelii* Kollman [1]; ?*Acteonella elongata* Kollman [4]; *Neocylindrites minutus* (Stolizcka) [2]. **Ammonite:** *Nostoceras (Nostoceras) major* Kennedy & Cobban [1]. **Nautiloids:** *Deltoidonautilus salisfilius* sp. nov. [9]. **Corals:** *Cunnolites* sp. [6]; cerioid colonies (2 genera) [3]. **Sponges** [7].

Bed 10. Bivalves: *Vaccinites oppeli* (Douvillé) [abundant, in situ].

Qarn Murrah

Rudist level near top of section. Bivalves: *Osculigera* cf. *vautrinioides* Vögel [32]; *Vaccinites vesiculosus* (Woodward) [13];?*Vaccinites loftusi* (Woodward) [3]; *Glabrobournonia arabica* Morris & Skelton, sp. nov. [16]; *Pseudosabinia* aff. *klinghardti* (Boehm) [1]; *Pseudopolyconites* aff. *parvus* Milovanovic [1]; *Colveraia variabilis* Klinghardt [1]. **Corals:** *Cunnolites* sp. [2]; cerioid colonies (2 genera) [3].

Qarn Mulayh

Lower part. Bivalves: *Pironaea* cf. *polystylus* Pirona [3]; *Durania* form A [2]; *Durania* sp. [1].

7·7 m below the top of the section. Bivalves: *Torreites sanchezi (Douvillé) milovanovici* Grubic [3].

Unspecified level. Bivalves: *Colveraia variablilis* Klinghardt [1].

Bull. nat. Hist. Mus. Lond. (Geol.) **51**(2):121–240 Issued 30 November 1995

Late Campanian-Maastrichtian echinoids from the United Arab Emirates-Oman border region

ANDREW B. SMITH

Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD

CONTENTS

SYNOPSIS. Forty-five echinoid species, 14 of them new, are described from the Maastrichtian Simsima Formation exposed along the western margins of the North Oman Mountains. The stratigraphic distribution of over 2,500 individual fossil echinoids has been recorded and used to assess echinoid abundance quantitatively and identify recurrent assemblages of species. Although approximately equal numbers of regular and irregular echinoid species are known, irregular echinoids greatly outnumber regulars in abundance. Furthermore, most species are rare, with just five making up more than 67% of the total collection. Regular echinoids are divisible into four ecological groups, ranging from hard-ground dwellers living within active wave-surge environments, to herbivores living in protected subtidal soft-bottom environments. Five ecological groups of irregular echinoid are distinguished, largely on the basis of their inferred feeding strategies. Seven echinoid assemblages are distinguished and their palaeoecological setting interpreted on the basis of the autecology of included species, associated macrofauna and lithofacies evidence. One new genus of Goniopygidae, *Mimiosalenia*, is described and the following new species are erected: *Prionocidaris? emiratus*, *Heterodiadema buhaysensis*, *Salenia microprocta*, *Goniopygus arabicus*, *Mimiosalenia quinquetuberculata*, *Codiopsis lehmannae*, *Hattopsis paucituberculatus*, *Circopeltis? emiratus*, *Phymechinus? perplexus*, *Coptodiscus magniproctus*, *Petalobrissus rawdahensis*, *Nucleopygus magnus*, *Stigmatopygus? pulchellus*, *Arnaudaster cylindriformis*.

INTRODUCTION

Late Cretaceous echinoid faunas, though well-documented in both Europe and America, remain relatively little studied elsewhere in the world. Those of the Middle East are particularly poorly known. Much of our knowledge of Tethyan late Cretaceous echinoid faunas comes from the major monographic works of the last century such as those dealing with Algeria (Cotteau *et al.* 1881), Iran (Cotteau & Gauthier 1895; Gauthier 1902) and Baluchistan (Noetling 1897), all of which are now in great need of revision and updating. Additional major late Cretaceous faunas were described during the early part of this century from Libya (Checchia-Rispoli 1930, 1931a,b, 1932a,b, 1933) and from Madagascar (Cottreau 1908; Lambert 1933).

Until recently the late Cretaceous faunas of the Arabian Peninsula remained virtually unknown. Duncan (1865) described a few Cenomanian echinoids from south eastern Oman, while Lees (1928) described two new late Cretaceous echinoid species from north western Oman. Clegg (1933) described a large number of echinoids from the Persian Gulf, but only two of these were Cretaceous, and neither appears to be late Cretaceous in age.

The first indication of the rich late Cretaceous echinoid fauna of the Arabian Peninsula came with the publication of Kier's (1972) monograph on the Mesozoic and Tertiary echinoids around Riyadh, Saudi Arabia. In this work he described 11 species from the Campanian-Maastrichtian Aruma Formation, six of which were new to science and the remainder representing species already described by Cotteau & Gauthier (1895) and Gauthier (1902) from southern Iran. Subsequently, Ali (1989, 1992a,b) documented 20 echinoids, including seven new species, from the Simsima and Qahlah Formations of the western Oman Mountains. Smith (in Skelton *et al.* 1990) gave some preliminary records of the echinoid fauna from these beds and Roman *et al.* (1989) gave a preliminary report on the Cretaceous echinoids of the Dhofar region, Oman, including four Campanian/Maastrichtian species.

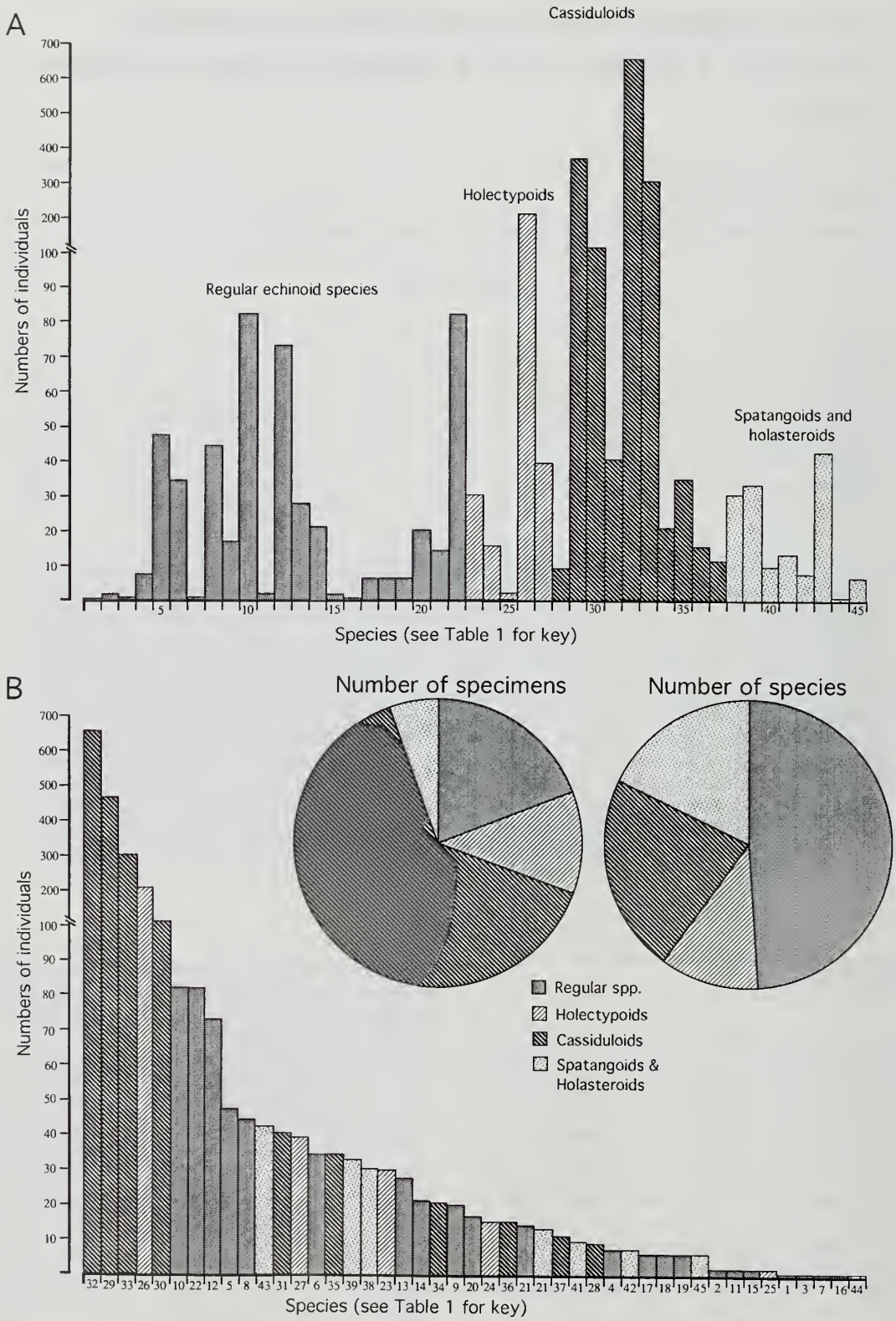


Fig. 1 Relative abundance of species collected from the Maastrichtian Qahlah and Simsima Formations along the United Arab Emirates-Oman border region (based on *ca.* 2,500 individuals). Species 1–45 are listed in Table 1. Shading distinguishes the four major taxonomic groups of echinoids. **A**, species arranged systematically. **B**, species arranged in order of specimen abundance. Pie diagrams represent the number of individuals and number of species for each major taxonomic group.

Table 1. Echinoid species collected from the Qalah and Simsima Formations exposed in the Jebels along the Oman-United Arab Emirates border region.

Class Echinoidea Leske, 1778
Subclass Cidaroidea Claus, 1880
Order Cidaroida Claus, 1880
Family Rhabdocidaridae Lambert, 1900
1. **Gen. et sp. indet.**
Family Cidaridae Gray, 1825
Genus *Prionocidaris* Agassiz, 1863
2. ***Prionocidaris morgani* (Gauthier, 1902)**
3. ***Prionocidaris? emiratus* sp. nov.**
Subclass Euechinoidea Bronn, 1860
?Cohort Diadematacea Duncan, 1889
?Order Diadematoida Duncan, 1889
Family Heterodiadematidae Smith & Wright, 1993
Genus *Heterodiadema* Cotteau, 1864
4. ***Heterodiadema buhaysensis* sp. nov.**
Cohort Echinacea Claus, 1876
Plesion (Order) Orthopsida Mortensen, 1942
Family Orthopsidae Duncan, 1889
Genus *Orthopsis* Cotteau, 1864
5. ***Orthopsis miliaris* (d'Archiac, 1835)**
Order Calycina Gregory, 1900
Family Saleniidae Agassiz, 1838
Genus *Salenia* Gray, 1835
6. ***Salenia nutrix* Peron & Gauthier, 1881**
7. ***Salenia microprocta* sp. nov.**
Order Arbacioida Gregory, 1900
Family Goniopygidae Smith & Wright, 1993
Genus *Goniopygus* Agassiz, 1838
8. ***Goniopygus arabicus* sp. nov.**
Genus *Mimiosalenia* gen. nov.
9. ***Mimiosalenia quinquetuberculata* sp. nov.**
Family Glyphopneustidae Smith & Wright, 1993
Genus *Glyphopneustes* Pomel, 1883
10. ***Glyphopneustes hattaensis* Ali, 1992**
Family Arbaciidae Gray, 1835
Genus *Codiopsis* Agassiz, 1840
11. ***Codiopsis lehmannae* sp. nov.**
Genus *Hattopsis* Ali, 1992
12. ***Hattopsis sphericus* Ali, 1992**
13. ***Hattopsis paucituberculatus* sp. nov.**
Genus *Noetlingaster* Vredenberg, 1911
14. ***Noetlingaster paucituberculatus* (Noetling, 1897)**
15. ***Noetlingaster emiratescus* Ali, 1989**
16. ***Noetlingaster*? sp.**
Order Phymosomatoida Mortensen, 1904
Family Phymosomatidae Pomel, 1883
Genus *Phymosoma* Haime, 1853
17. ***Phymosoma hexoaporum* Lambert, 1927**
Genus *Actinophyma* Cotteau & Gauthier, 1895
18. ***Actinophyma spectabile* Cotteau & Gauthier, 1895**
Genus *Plistophyma* Peron & Gauthier, 1881
19. ***Plistophyma asiaticum* Cotteau & Gauthier, 1895**
Family Stomechinidae Pomel, 1883
Genus *Circopeltis* Pomel, 1883
20. ***Circopeltis? emiratus* sp. nov.**
Genus *Phymechinus* Desor, 1856
21. ***Phymechinus? perplexus* sp. nov.**
Genus *Echinotiara* Pomel, 1883
22. ***Echinotiara perebaskinei* Lambert, 1929**
Cohort Irregularia Latreille, 1825
Order Holectypoida Duncan, 1889
Family Holectypidae Lambert, 1899
Genus *Coenholectypus* Pomel, 1883
23. ***Coenholectypus inflatus* (Cotteau & Gauthier, 1895)**
24. ***Coenholectypus* cf. *baluchistanensis* (Noetling, 1897)**
Genus *Coptodiscus* Cotteau & Gauthier, 1895
25. ***Coptodiscus magniproctus* sp. nov.**
Family Conulidae Lambert, 1911
Genus *'Globator'* Agassiz, 1840
26. ***'Globator' bleicheri* (Gauthier, 1889)**
Genus *Conulus* Leske, 1778
27. ***Conulus douvillei* (Cotteau & Gauthier, 1895)**
Order Cassiduloida Claus, 1880
Family Clypeolampadidae Kier, 1962
Genus *Vologesia* Cotteau & Gauthier, 1895
28. ***Vologesia rawdahensis* Ali, 1989**
Family Faujasiidae Lambert, 1905
Genus *Faujasia* d'Orbigny, 1856
29. ***Faujasia eccentripora* Lees, 1928**
Genus *Zuffardia* Checchia-Rispoli, 1917
30. ***Zuffardia morgani* (Cotteau & Gauthier, 1895)**
Unnamed family
Genus *Pygurostoma* Cotteau & Gauthier, 1895
31. ***Pygurostoma morgani* Cotteau & Gauthier, 1895**
Family Cassidulidae Agassiz & Desor, 1847
Genus *Petalobrissus* Lambert, 1916
32. ***Petalobrissus rawdahensis* sp. nov.**
33. ***Petalobrissus* cf. *setifensis* (Cotteau, 1866)**
34. ***Petalobrissus linguiformis* (Peron & Gauthier, 1881)**
Genus *Stigmatopygus* d'Orbigny, 1856
36. ***Stigmatopygus? pulchellus* sp. nov.**
Genus *Nucleopygus* Agassiz, 1840
35. ***Nucleopygus magnus* sp. nov.**
Family Echinolampadidae Gray, 1851
Genus *Arnaudaster* Lambert, 1918
37. ***Arnaudaster cylindriformis* sp. nov.**
Order Holasteroida Durham & Melville, 1957
Family Holasteridae Pictet, 1857
Genus *Hemipneustes* Agassiz, 1836
38. ***Hemipneustes compressus* Noetling, 1897**
39. ***Hemipneustes persicus* Cotteau & Gauthier, 1895**
40. ***Hemipneustes arabicus* Ali, 1989**
Order Spatangoida Claus, 1876
Family Hemiasteridae Clark, 1917
Genus *Hemiaster* Agassiz, *in* Agassiz & Desor, 1847
41. ***Hemiaster hattaensis* Ali, 1989**
42. ***Hemiaster paronai* Checchia-Rispoli, 1921**
Genus *Mecaster* Pomel, 1883
43. ***Mecaster victoris* (Lambert, 1932)**
Family Schizasteridae Lambert, 1905
Genus *Linthia* Desor, 1853
44. ***?Linthia sudanensis* (Bather, 1904)**
Genus *Proraster* Lambert, 1895
45. ***Proraster geayi* Cottreau, 1908**

Our field collecting in this region has more than doubled the known fauna of late Cretaceous echinoids, making it one of the most diverse assemblages of this age anywhere in the world. Much of the material is well preserved, allowing plating details to be recorded in many species and genera for the first time. Forty four species are recognized (Table 1) and sufficient material has been collected (over 2,500 specimens) to allow a detailed biometric study of most species. Furthermore, bed by bed collecting has enabled me to recognize recurrent assemblages and to place these into their palaeoenvironmental setting, something that has never previously been attempted.

RELATIVE ABUNDANCES OF SPECIES

A total of 2585 specimens were collected and identified to species level, allowing a quantitative assessment of species abundance. This is not entirely accurate in comparison with a previous study of echinoid abundance in the Cenomanian (Smith 1988) where every specimen seen was collected, because the three or four most abundant species are surely undercollected. A few species (e.g. *Petalobrissus rawdahensis* at Jebel Rawdah, section 2, or '*Globator*' *bleicheri* at Jebel Buhays) were so abundant that only a proportion of the observed specimens were eventually collected. There is therefore a bias towards the rarer species. Nevertheless, a number of general conclusions can be drawn from the distributional and abundance data that have been collected.

(a) There are approximately equal numbers of regular and irregular echinoid species (22 regular, 23 irregular) (Fig. 1B). A similar ratio of regular to irregular species is characteristic of the present day biota (Kier 1977) and for extensive collections from the Cenomanian of Great Britain and France (Smith 1988, Neraudeau & Moreau 1989). Amongst the irregular echinoids, cassiduloids (10 species) are more diverse than holectypoids (5 species), spatangoids (5 species) or holasteroids (3 species).

(b) Irregular echinoids greatly exceed regular echinoids in numbers of specimens (Fig. 1B). In total 499 specimens of regular echinoid were collected (19%), and this is likely to overestimate their true relative abundance, since the five most common echinoids were all irregular species and are likely to have been significantly undercollected. This compares well with previous studies, where Smith (1988) found between 10–20% of the total number of echinoid specimens collected (1800 individuals) from the Cenomanian of Wilmington were regular species, and with Neraudeau & Moreau (1989) who reported 22.8% of 5133 individuals collected from the Cenomanian of North Aquitaine were regular species. Therefore regular echinoids achieve a similar species diversity to irregular echinoids, but occur in much lower absolute diversity.

(c) Most species are rare. In terms of numbers of individuals, just five species make up more than 67% of the total collection (Fig. 1A). Four of these five species are cassiduloid, the fifth (8% of the total) is the holectypoid '*Globator*'. The most abundant species are cassiduloids and two of the three species of *Petalobrissus* together form more than 36% of the total number of individuals collected. In reality these species are even more dominant, since they were certainly undercollected in comparison to rare species, possibly by as much as a factor of two.

In comparison, the most abundant regular echinoid species (*Echinotiara perebaskinei* and *Glyphocyphus hattaensis*) represent only 3.2% of the total collection each, and the the most common spatangoid (*Mecaster victori*) and holasteroid (*Hemipneustes persicus*) represent a mere 1.6% and 1.4% respectively of the total collection.

ECHINOID PALAEOECOLOGY

Echinoids are adapted to live in a wide range of habitats and the relationship between skeletal structure, habitat and mode of life is now relatively well understood. Consequently they are an excellent group to use as palaeoenvironmental indicators. Virtually nothing is known about the late Cretaceous palaeoecology of echinoids in tropical carbonate shelf environments, and the Oman Mountains collection described here provides the first such opportunity to assess echinoid distribution and faunal associations quantitatively.

Before discussing the assemblages that can be recognized and their palaeoenvironmental setting, it is necessary to look at the detailed functional morphology of the different taxa. Each has a preferred habit and life-style that is partially reflected and can be deduced from the skeletal morphology (e.g. Smith 1984).

1. *Regular echinoids*. All regular echinoids live epifaunally, but can be differentiated into a number of ecological groups based on their skeletal morphology.

(a) Hard-ground dwellers living within the zone of active wave surge (0–5 m depth). This includes *Codiopsis*, *Phymechinus*, *Circopeltis* and *Echinotiara*. These forms are characterized by their flat oral surface and enlarged phyllodes composed of P3/P4-type pore-pairs (Smith 1978). They also typically have dense or modified aboral pore-pairs indicative of specialized respiratory tube-feet. The broad, flat base and numerous, large oral tube-feet are features characteristic of present-day echinoids living on rocky surfaces within the zone of active wave surge. Large and strong oral tube-feet are necessary to provide adhesion in a turbulent environment. Modern analogues would be *Arbacia*, *Anthocidaris*, *Heliocidaris* or *Stomopneustes*, all of which are coastal species living within the first few metres on rock or other hard ground surfaces. They are rock grazers, feeding on filamentous or fleshy algae which they obtain by rasping hard substrata.

(b) Hard-ground dwellers living subtidally within the top few metres of water but subject to limited wave surge only. Here I include only *Goniopygus*. *Goniopygus* has moderately strong phyllodes, a depressed profile though without a broad flat oral surface, and well-developed aboral respiratory tube-feet (to judge from its pore-pairs). The aboral respiratory tube-feet suggest it had a relatively high metabolic rate and therefore lived in the shallow, warmest waters. It had strong oral tube-feet for adhesion, but these were not as highly developed as those of species in group (a) and it seems unlikely that *Goniopygus* could have lived in fully exposed habitats.

(c) Shallow water (*ca.* 2–10 m) forms living in more protected environments, within wave base, but not subject to strong currents or wave surge. These echinoids might typi-

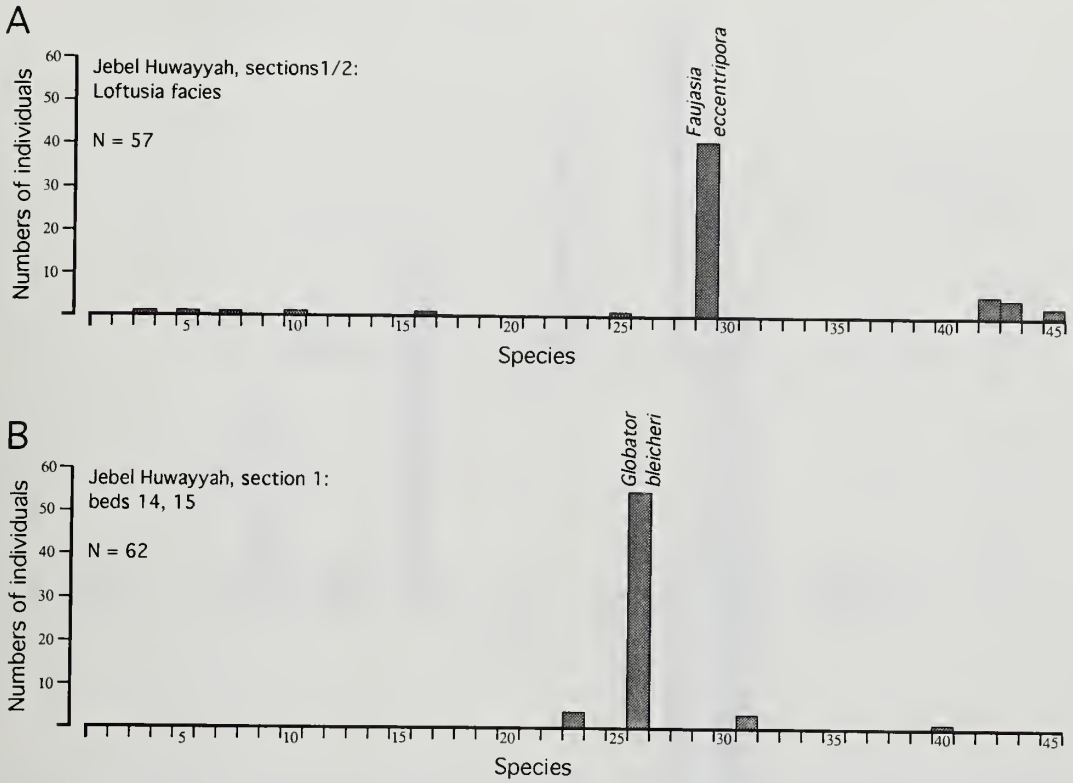


Fig. 2 Echinoid species abundances within specific units at Jebel Huwayyah. **A**, fauna from beds 10–12, section 1 and beds 1–6, section 2 (*Loftusia*-rich facies). **B**, fauna from beds 14 and 15, section 1. Species are listed numerically along the x-axis as in Table 1. N = total number of specimens collected.

cally be expected to have lived on or close to firm bottoms, i.e. either rocky or reefal knolls or stabilized sedimentary substrata. Taxa included here are *Orthopsis*, *Phymosoma*, *Plistophyma*, *Actinophyma*, *Mimiosalenia*, and *Glyphopneustes*. These echinoids all have a depressed profile and slight phyllodes, and often have increased densities of aboral pore-pairs, possibly specialized for gaseous exchange. Their spines are moderate to long. Modern equivalents, such as *Lytechinus* or *Temnopleurus* live in and around hardground substrata in reasonably well-protected habitats. They are predominantly grazers, feeding on encrusting or boring algae or plants and removing upright algae down to the substratum. Those with no phyllode development and invaginated peristomes are likely to have been grazers, whereas those with oral phyllodes and a flat peristome were probably raspers.

Heterodiadema is a large, motile diadematoid-like echinoid with long spines whose closest modern counterparts are forms such as *Centrostephanus* or *Diadema*, found living in algal turf (dense stands of filamentous algae) or in amongst thickets in the reef flat environment (Birkeland 1989).

The cidarids *Rhabdocidaris* and *Prionocidaris* probably belong to this category. They are clearly shallow-water forms because of their well-developed respiratory tube-feet (conjugate pore-pairs), but are globular in profile and lack phyllodes. They would have been confined to the most protected of the shallow-water habitats, along with *Heterodiadema*. Cidarids and diadematoids are rather generalist feeders, preferentially grazing on animals and plants, but also able to take up bottom material (Birkeland 1989).

(d) Protected subtidal (10 m plus) soft-bottom substrata below active wave base. *Noetlingaster*, *Hattopsis* and *Salenia* are all globular forms lacking aboral specialised respiratory tube-feet. *Noetlingaster* closely resembles the present-day *Echinus* or *Tripneustes* in morphology and presumably lived in much the same way, found largely on sandy substrata of lagoons or below active wave-base moving over stable sedimentary bottoms or living within algal stands. These forms are predominantly herbivorous browsers, cropping exposed algae and taking loose bottom material. The extreme globular shape of *Hattopsis* is matched by that seen in some present day temnopleurids such as *Microcyphus* and, like those echinoids, it may have lived within algal turf, attached to and enveloped by fronds of filamentous algae.

Irregular echinoids. These too can be divided into a number of discrete ecological groups based on observed skeletal characteristics.

(e) Infaunal medium-fine sand-grade burrowers which are selective deposit feeders using penicillate tube-feet around the mouth to pick up food particles from sediment of the burrow floor. Here I include *Hemiaster* and *Mecaster*. Both have globular tests with no real frontal sulcus. Pore differentiation shows that funnel-building tube-feet would have been present in ambulacrum III adapically, and subanally in the posterior ambulacra also. These heart urchins clearly lived infaunally within relatively poorly permeable, rather fine-grained sediment. An apical funnel is required by infaunal spatangoids living in finer-grained sediments, as is the aboral fasciole (which is essential for maintaining a water-filled space surrounding the test). The lack of specialization of the

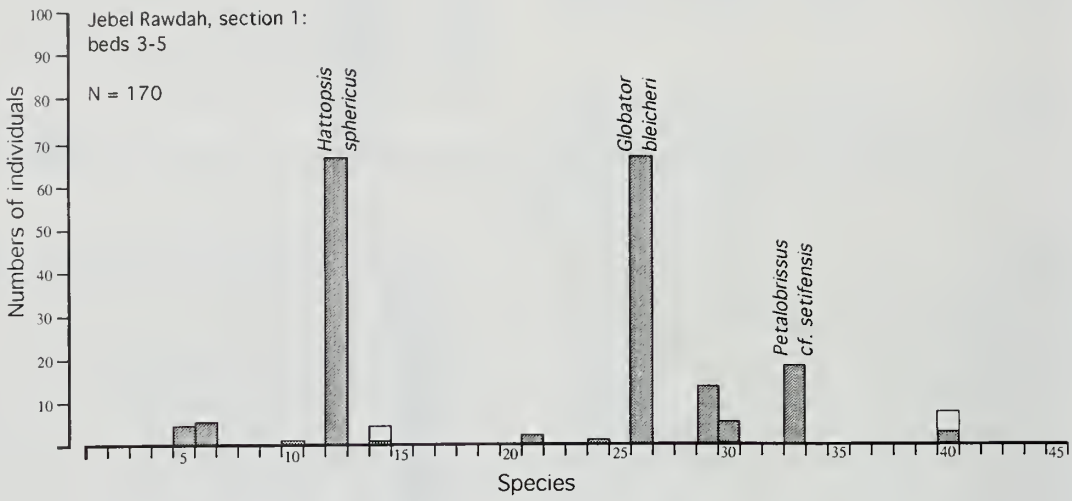


Fig. 3 Echinoid species abundances within beds 3–5 at Jebel Rawdah, section 1. Species are listed numerically along the x-axis as in Table 1. N = total number of specimens collected. Unshaded box = fragments only.

frontal groove implies that all food particles were derived from within the sediment, not from the sediment/water interface.

(f) Infaunal medium-fine sand-grade burrowers, selective deposit feeders harvesting organic material from the sediment-water interface. Only *Proraster* falls into this group. It has a deep, highly specialized frontal groove which is characteristic of those modern taxa feeding by means of a mucus-string. It is very similar to the extant *Schizaster*, and presumably lived in very much the same way. The pore-pairs in ambulacrum III are specialized and indicate the presence of highly developed funnel-building tube-feet. There is little doubt that *Proraster* lived infaunally, feeding on detritus from the water/sediment interface that cascaded down the funnel. The implication (though untested as far as I am aware) is that *Proraster* is adapted for life in more organic-poor sediments than either *Hemiaster* or *Mecaster* since it preferentially harvests surface detritus. The well-developed petals show that *Proraster* was still a relatively shallow-water form.

(g) Shallow infaunal or semi-infaunal ploughers in stable, unconsolidated bottoms. Bulk deposit feeders harvesting sediment at or close to the water interface. Only *Hemipneustes* falls into this catagory. *Hemipneustes* has a well-developed anterior groove with specialized grill spines and tube-feet. Sediment would have entered the frontal groove adapically and passed to the mouth via a mucous string running down ambulacrum III. The lack of protection for petal tube-feet, and the asymmetry of the petals implies that the surrounding sediment was highly permeable and that the urchins lived only relatively shallowly burried.

(h) Mobile high permeability (low fines) unconsolidated medium-coarse sands: infaunal bulk sediment swallowers. This category includes *Petalobrissus*, *Nucleopygus*, *Pygurostoma* and *Stigmatopygus*. These urchins most closely resemble the present day *Apatopygus*, which is a bulk sediment swallower. They have small phyllodes around the peristome, with moderately well developed bourrelets (specialized regions of dense spines used for manipulating sand-grade particles into the peristome. Their large periproct and anal sulcus suggests they had to cope with copious faecal discharge. They are small, depressed forms streamlined for moving through loose sediment and have well-developed petals.

Vologesia and *Arnaudaster* have similar phyllodes but are much larger animals, more closely resembling *Echinolampas*. *Echinolampas* is found today in subtidal (5–20 m) depths living infaunally in shell-sands (e.g. Thum & Allen 1975). *Petalobrissus* is likely to be adapted for more mobile sediments, i.e. for shallow subtidal shoals.

(i) Mobile, permeable unconsolidated sands: selective, infaunal deposit feeders. Here I place *Zuffardia* and *Faujasia*. Both have small peristomes, surrounded by moderately well-developed phyllodes, and with slight bourrelet development. They both have rather small, posteriorly placed periprocts, and from this it would appear that they were rather more selective deposit feeders than *Petalobrissus* and other related taxa. They have large petals and clearly lived infaunally, because of their rounded shape. However, they could only have done so within highly permeable sands, finer sediments being insufficiently porous to allow sufficient water flow past the well-developed petals.

(j) Infaunal selective particle feeders living within coarse,

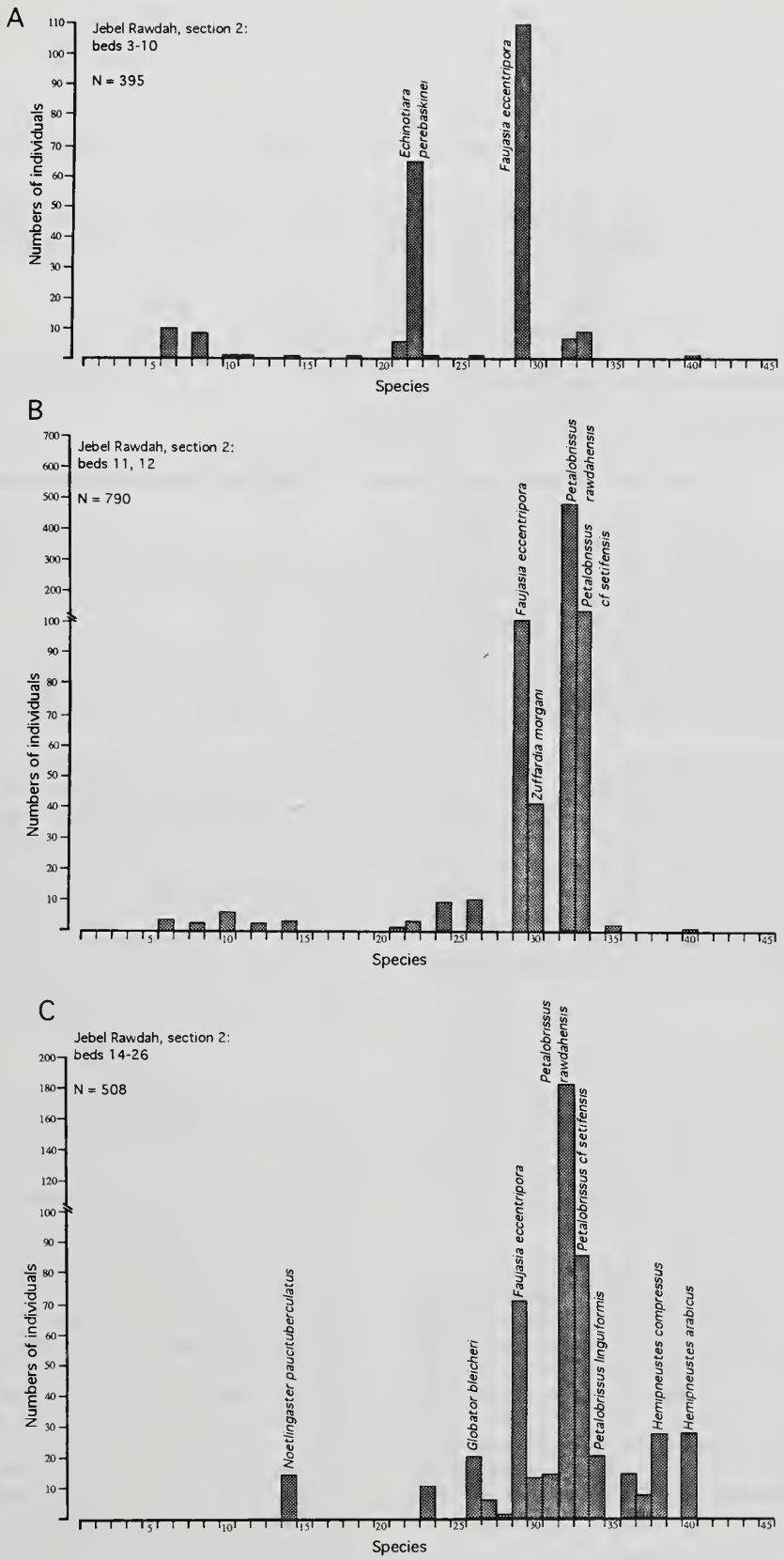


Fig. 4 Echinoid species abundances within units at Jebel Rawdah, section 2. **A**, fauna from beds 3–10; **B**, fauna from beds 11 and 12; **C**, fauna from beds 14–26. Species are listed numerically along the x-axis as in Table 1. N = total number of specimens collected.

Table 2 Inferred palaeoenvironmental settings for the late Cretaceous succession of the Oman-United Arab Emirates border region. The common echinoid taxa found in each habitat are listed, together with indications of their probable life style.

Habitat A nearshore hardground dwellers living in zone of active wave surge.
(i) Hardground grazers: *Echinotiara perebaskinei*, *Phymechinus? perplexus*, *Codiopsis lehmannae*.

Habitat B nearshore hardground dwellers living in more protected environments (perireefal).
(i) Hardground grazers: *Goniopygus arabicus*.

Habitat C subtidal protected environments within normal wave base; mixed cobble and sand substrata with nearby level-bottom reefal thickets.
(i) Epifaunal grazers: *Glyphopneustes hattaensis*, *Mimiosalenia quinquetuberculata*, *Goniopygus arabicus*, *Phymosoma hexoaporum*.
(ii) Epifaunal browsers: *Circopeltis? emiratus*, *Heterodiadema buhaysensis*, *Orthopsis miliaris*, *Hattopsis paucituberculatus*, *Plistophyma asiaticum*.
(iii) Epifaunal generalists: *Prionocidaris morgani*, *Prionocidaris? emiratus*, *Salenia nutrix*, *Salenia microprocta*.
(iv) Infaunal grazers/detritivores: '*Globator*' *bleicheri*, *Conulus douvillei*, *Coenholectypus* cf. *baluchistanensis*.
(v) Infaunal bulk sediment swallowers: *Nucleopygus magnus*, *Pygurostoma morgani*.
(vi) Infaunal selective deposit feeders: *Vologesia rawdahensis*, *Arnaudaster cylindriformis*, *Hemiaster hattaensis*.

Habitat D Shore-face sand flats at or within normal wave base.
(i) Bulk sediment swallowers: *Petalobrissus rawdahensis*, *P.* cf. *setifensis*.
(ii) Selective deposit feeders: *Zuffardia morgani*, *Faujasia eccentripora*.
(iii) Infaunal generalist detritivores: '*Globator*' *bleicheri*, *Coenholectypus* cf. *baluchistanensis*.

Habitat E Broad shallow, open shelf subtidal sand flats, within normal wave base (2–10 m) but distant from the platform margin and thus relatively protected.
(i) Epifaunal grazers: *Noetlingaster paucituberculatus*, *Hattopsis sphericus*.
(ii) Semi-infaunal selective deposit feeders: *Hemipneustes* spp.
(iii) Infaunal selective deposit feeders: *Mecaster victoris*, *Hemiaster paronai*, *Stigmatopygus? pulchellus*, *Faujasia eccentripora*.
(iv) Infaunal bulk sediment swallowers: *Petalobrissus rawdahensis*, *P.* cf. *setifensis*, *Pygurostoma morgani*.

Habitat F Deeper-water (20 m plus) platform basinal muddy sands, below normal wave base.
(i) Epifaunal grazers: possibly *Actinophyma spectabile*.
(ii) Infaunal selective deposit feeders, harvesting detritus from the sediment/water interface: *Proraster geayi*.

permeable sands behind fringing reefs in 0–10 m water depth. *Conulus*, '*Globator*' and *Coenholectypus* belong here, though the highly inflated *C. inflatus* may have reverted to a primarily epifaunal mode of life, below normal wave base. *Globator* closely resembles the present day *Echinoneus* whose ecology was described by Rose (1976). *Echinoneus* lives beneath coral debris in coarse shell-sands passing suitable grains into its peristome by means of its tube-feet.

Inferred depths and habitats for typical Omani echinoids are tabulated in table 2.

ECHINOID ASSEMBLAGES

Because careful count of the number of specimens collected for each taxon was kept it is possible to identify recurring assemblages. The following seven assemblages are differentiated here.

(1). Conulid/arbacioid assemblage. An abundance of *Conulus* and '*Globator*' which is usually accompanied by a diverse mixture of regular echinoids, notably by the arbacioids *Goniopygus*, *Glyphopneustes*, *Mimiosalenia* and *Hattopsis*. Other taxa making up a smaller component of the fauna include *Phymosoma*, *Nucleopygus* and *Pygurostoma* (Figs 2B, 3, 5B, 6).

This assemblage is characteristic of the lower beds of the Simsima Formation at Jebel Buhays, Jebel Thanais, Jebel Faiyah, and Jebel Huwayyah. It is typically developed with the income of relatively coarse, carbonate bioclastic sands in the succession.

Interpretation: the conulid/arbaciid assemblage has a very high diversity of regular echinoids that would have preferred stabilized bottoms in shallow water conditions protected from the influence of strong wave action. The presence of '*Globator*' implies that the sediment was unconsolidated, permeable and rather coarse, while horizons with an abundance of *Hattopsis* might suggest the presence of nearby algal stands. The abundance and diversity of regular echinoids (most of which are algivore grazers) implies a mixture of environments were close by, ranging from rocky (?patch-reef, as seen at Jebel Faiyah) to stabilised sedimentary bottoms with algal stands. The palaeoenvironment is therefore most likely to represent a shallow (5–10 m) backreef or leaward environment that supports a high algal diversity.

(2). *Echinotiara/Faujasia/Phymechinus* assemblage. An assemblage which includes a number of rarer regular echinoids absent from most other assemblages (e.g. *Codiopsis*, *Phymechinus*). *Faujasia* is the only common element found at other levels, but no other irregular echinoid occurs in any abundance (Fig. 4A).

This assemblage is best developed at Jebel Rawdah section 2, in the basal calcarenitic beds with associated coral/rudist debris.

Interpretation: this assemblage is dominated by hardground, shallow-water (0–5 m) epifaunal regular echinoids (*Echinotiara*, *Phymotaxis*, *Codiopsis*) adapted for life in strong wave-surge environments. Clearly none are preserved in situ, but have been transported into immediately adjacent basins of sediment accumulation, along with coral and stromatoporoid debris and hippuritid rudist debris indicative of reef habitat. Transportation has not been far, otherwise much more disintegration of tests might be expected. The occurrence of large blocks of rolled coral with stromatoporoid and rudist debris at Jebel Rawdah section 3, implies that the deposits accumulated close to actual reefal framework. *Fauja-*

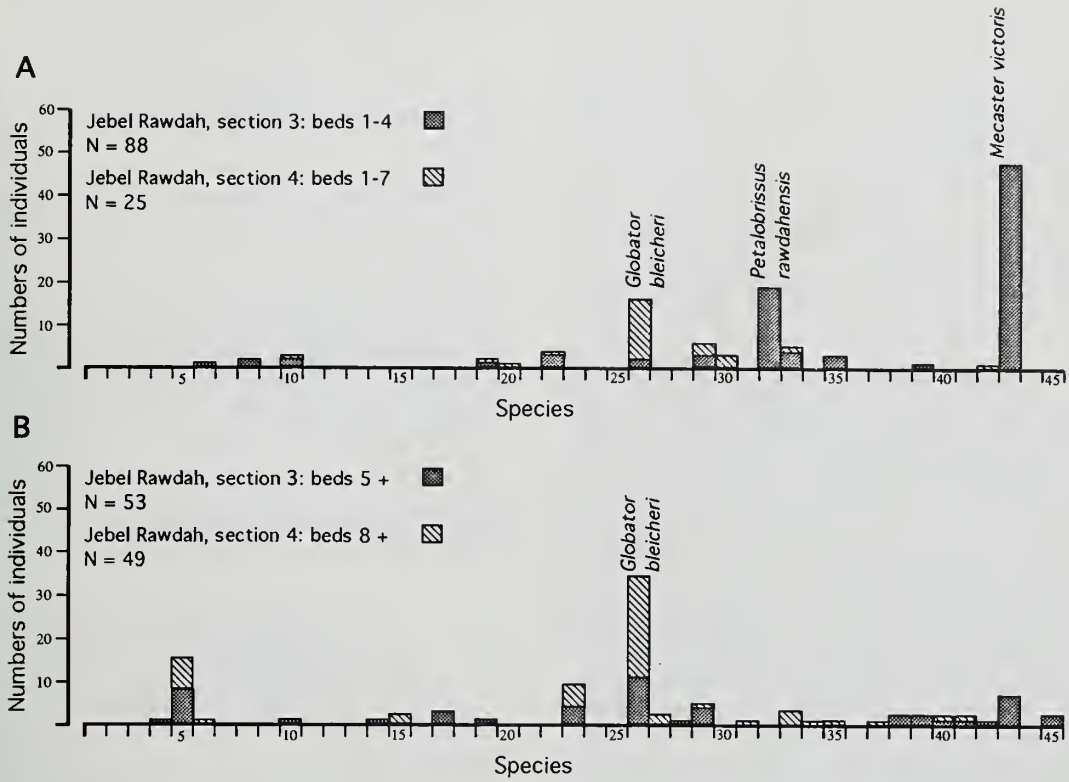
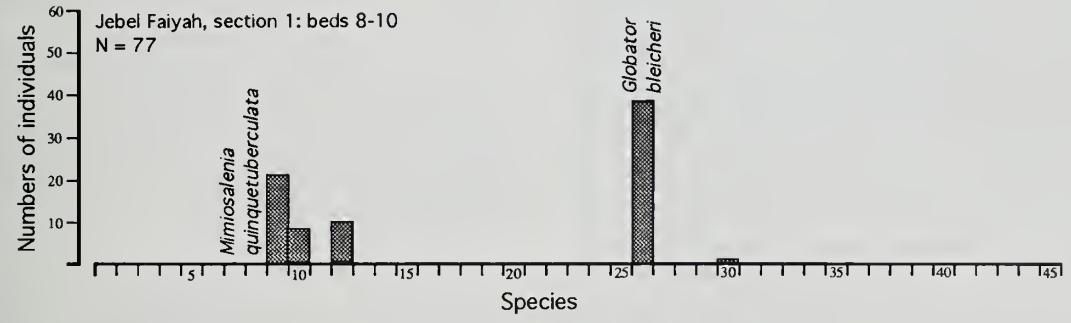


Fig. 5 Echinoid species abundances within units at Jebel Rawdah, sections 3 and 4. **A**, fauna from lower beds; **B**, fauna from higher beds. Species are listed numerically along the x-axis as in Table 1. N = total number of specimens collected.



ig. 6 Echinoid species abundances within units at Jebel Faiyah, section 1, beds 8–10. Species are listed numerically along the x-axis as in Table 1. N = total number of specimens collected.

a may be the only in situ echinoid for the depositional nvironment, living within the surrounding sand-fields in an nmediately subtidal environment, although none is pre-:rved with associated spines. *Goniopygus* is found in asso-ation, and it probably lived amongst the tallus derived from e reef crest rather than on the crest itself.

) *Petalobrissus* assemblage. At certain levels of coarse, nconsolidated orbitoline limestones *Petalobrissus* occurs in ge abundance, accompanied by much smaller numbers of her infaunal echinoids (*Zuffardia*, *Faujasia*, *Coenholecty-s* and '*Globator*'). Rare *Noetlingaster* are the only regular hinoids encountered (Fig. 4B).

This assemblage is seen only in the lower part of the section (beds 11–13) at Jebel Rawdah, section 2.

Interpretation: this assemblage is composed entirely of small, bulk sediment swallowers and is suggestive of shallow subtidal unconsolidated and well-washed sand flats free of algae, presumably subject to constant disturbance. The beds can thus be envisaged as shallow (0–10 m) orbitoline sand flats developed behind a fringing reef. The abundance of individuals suggests that this was a region of relatively high productivity.

(4) *Hemipneustes/Noetlingaster* assemblage. The abundance of large infaunal selective deposit feeders, notably *Hemip-*

neustes and *Pygurostoma*, characterises this assemblage. Usually *Noetlingaster*-rich levels alternate with holasterid-rich levels, so it may not be entirely correct to treat these as one assemblage, though they occur intermixed within the same lithofacies. All the species are large in comparison to those elsewhere. This assemblage typifies the upper beds of section 2, Jebel Rawdah (Fig. 4C).

Interpretation: the *Hemipneustes/Noetlingaster* assemblage is composed of selective deposit feeders specialized for life within coarse, permeable sands, together with occasional specific bands of the large generalist algivore *Noetlingaster*. The dominance of large selective deposit feeders implies a relatively nutrient-starved environment where large-scale harvesting of the sediment/water interface is needed to exploit the food supply. Associated lithofacies evidence suggests that they were living within shallow-water (2–10 m) flat-bottom shoals, probably immediately infratidal. *Noetlingaster*, like *Echinus* in today's seas, may have been a generalist detritivore/algivorous browser. The environment of deposition is therefore envisaged as relatively quiet sedimentary level bottom shoals that lay not particularly deep but distant from the high productivity reef area or from more exposed platform margin conditions.

(5) *Faujasia* assemblage. Occasional, almost monospecific assemblages of *Faujasia* are found in calcified fine sands at Jebel Huwayyah near the base. In the associated *Loftusia*-rich levels there are also occasional *Hemiaster* and *Proraster*. These may be nearshore infratidal sands in relatively protected environments (Fig. 2A).

(6) *Mecaster* assemblage (Fig. 5A). Another virtually monospecific assemblage confined to a single level at Jebel Rawdah section 3. This time the only associated echinoids are the rare *Hemipneustes*.

(7) *Proraster* assemblage. Only *Proraster* is found in the highest, muddiest limestones of Jebel Huwayyah. The relatively fine-grade sediments and the absence of infaunal cassiduloids or holasteroids suggests that these beds may represent shelf-basinal deposits more than *ca.* 20 m deep. Only highly specialist infaunal forms such as *Proraster* could apparently cope with life in these relatively nutrient-poor mud-rich deposits.

PALAEOECOLOGICAL SYNTHESIS

The faunal succession records a relatively rapid deepening from beach boulder beds and sands through nearshore, high-energy, subtidal conditions with off-beach coral-rudist reefal patches to somewhat deeper-water conditions at or immediately beneath wave base. Maximum echinoid diversity is found in the shallow sand fields strewn with shell and coral debris surrounding coral thickets that formed at about wave-base around the shores of the uplifted ophiolite. Subsequent shallowing over the platform led to the creation of broad, shallow shoals supporting a low-diversity infaunal echinoid assemblage, dominated by holasteroids and cassiduloids. The only epifaunal echinoid here is *Noetlingaster*. The deepest water facies are probably those seen at the top of the section at Jebel Huwayyah, where only the infaunal spatangoid *Proraster* occurs.

SYSTEMATIC DESCRIPTIONS

Class **ECHINOIDEA** Leske, 1778
Subclass **CIDAROIDEA** Claus, 1880
Order **CIDAROIDA** Claus, 1880
Family **RHABDOCIDARIDAE** Lambert, 1900

Gen. et sp. indet. Pl. 1, fig. 1; Fig. 8

MATERIAL. A single specimen, comprising three interambulacral plates, BMNH EE3438.

OCCURRENCE. From the scree at Jebel Buhays, section 1; derived from the lowest 2–3 metres of the Simsima Formation.

DESCRIPTION. Three interambulacral plates, rather badly weathered, from the ambital region of the test. Plates are 18·7 mm wide by 8 mm tall and appear to have tesselate sutures. Each plate carries a single large tubercle with a circular, confluent areole that occupies the full height of the plate. The boss is surmounted by a broad, strongly crenulate

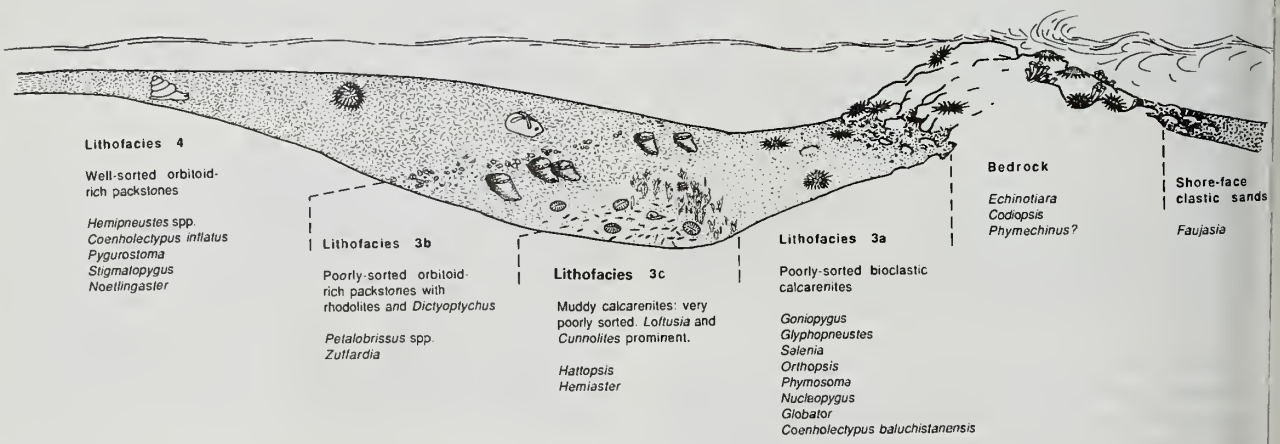


Fig. 7 Schematic reconstruction of the sea-floor in Maastrichtian times showing the range of environments represented in the study area. Sea urchins are illustrated in their probable mode of life and the inferred environmental ranges for key taxa are shown.

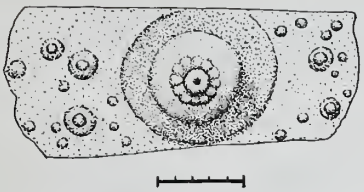


Fig. 8 Camera lucida drawing of an interambulacral plate of Rhabdocidaridae gen. et sp. indet., BMNH EE3438. Scale bar = 5 mm.

platform while the mamelon itself is rather small (1·2 mm diameter) and has a large central perforation. The primary tubercle lies subcentrally on the plate with a broad adradial and interradial platform on either side. The broad zones outside the areole of the primary tubercle have a few scattered secondary tubercles preserved, but are otherwise too abraded to retain any evidence of fine tuberculation that may have been present. It is clear from the distribution of the tubercles that are preserved that these regions were covered in a rather heterogenous and open array of various-sized tubercles.

REMARKS. The broad plates, confluent areoles, perforate crenulate tubercles and heterogeneous secondary tuberculation show this to be a member of the Rhabdocidaridae. It is impossible to place this specimen in any genus on the basis of such incomplete material. However, it most probably represents a species of *Rhabdocidaris* itself, judging from the size of the specimen and the coarseness of the secondary tuberculation.

Family **CIDARIDAE** Gray, 1825
Tribe **CIDARINI** Gray, 1825
Subtribe **PHYLLACANTHINA** Smith & Wright, 1989
Genus ***PRIONOCIDARIS*** Agassiz, 1863

Prionocidaris morgani (Gauthier, 1902) Pl. 1, figs 2–4; Fig. 9B

1902 *Rhabdocidaris (Leiocidaris) morgani* Gauthier: 145, pl. 20, figs 3–6.
1989 *Cidaris* cf. *scabra* Gauthier; Ali: 398, fig. 2.1.

TYPES. The syntypes are the two specimens described and figured by Gauthier. One is a more or less complete test 35 mm in diameter, the other an interambulacral segment. The whereabouts of this material is unknown: the specimens are not in the Morgan collection in the Museum National d'Histoire Naturelle, Paris.

MATERIAL STUDIED. Two specimens: BMNH EE3433, from the scree derived from the lowest beds of the Simsima Formation at Jebel Buhays, section 1; BMNH EE3435, loose in the scree at section 3b, Jebel Rawdah. A third fragment, EE3434, probably belonging to this species, was also found loose in the scree at Jebel Buhays.

OCCURRENCE. The syntypes come from the late Cretaceous ('Senonien superieur') of Louristan, Iran (Gauthier was unable to give a precise locality). In the United Arab Emirates the species comes from the Maastrichtian of Jebel Buhays and Jebel Rawdah.

DIAGNOSIS. A species of *Prionocidaris* with broad conjugate pore-pairs occupying more than half of the ambulacral plate width, and a perradial zone with a single primary tubercle and a row of tubercle-like granules, up to four abreast, on each plate. Interambulacra with well differentiated scrobicular circles and aligned extrascrobicular tuberculation.

DESCRIPTION. The following description is based on BMNH EE3433, the larger and better preserved of the two. The specimen comprises parts of two interambulacra and ambulacra. Interambulacral width at the ambitus is 23 mm, suggesting a test diameter of approximately 50 mm in life. Test height is 32 mm. The ambulacra are 6 mm in width and only slightly sinuous. The pore-pairs are very wide and conjugate (Pl. 1, fig. 4; Fig. 9B) and successive pore-pairs are closely spaced. The poriferous zone occupies approximately half of the plate width. There is a single primary tubercle with a mamelon immediately adjacent to each pore-pair. The remainder of the perradial zone is occupied by a row of large granules (non-mamelonate), some three or four abreast and organised into discrete vertical rows.

Interambulacral plates are relatively broad, an ambital plate being 13·1 mm by 9·4 mm in height. All plates, except the most adapical in each column, have a single large primary tubercle. This has a sunken areole 7·2 mm in diameter and a mamelon 2.2 mm in diameter (Pl. 1, figs 2, 4). Mamelons are perforate and the surrounding platform is non-crenulate. The primary tubercles lie offset towards the adradial suture leaving a broad interradial zone of miliary tuberculation. There is a clearly differentiated ring of scrobicular tubercles surrounding each areole. Extrascrobicular tuberculation is well developed with approximately 2 miliary granules abreast towards the adradial suture, eight abreast towards the interradial suture, and either a single row or no row developed adapical and adoral to the scrobicular circles. These extra-scrobicular tubercles are non-mamelonate and decrease in size towards

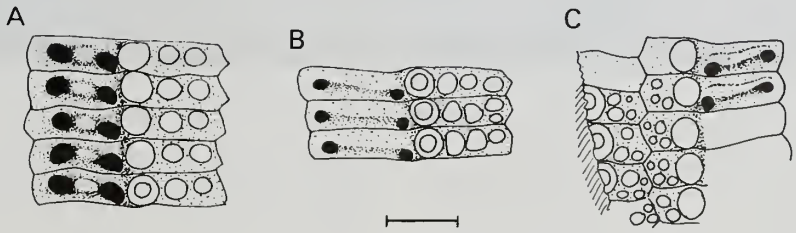


Fig. 9 Camera lucida drawings of ambital ambulacral plating in cidarid species. **A**, *Stereocidaris persica* (Cotteau & Gauthier), Museum d'Histoire Naturelle, Morgan Collection; **B**, *Prionocidaris morgani* (Gauthier), BMNH EE3433; **C**, *Prionocidaris? emiratus* sp. nov., BMNH EE3431. Scale bar = 1 mm.

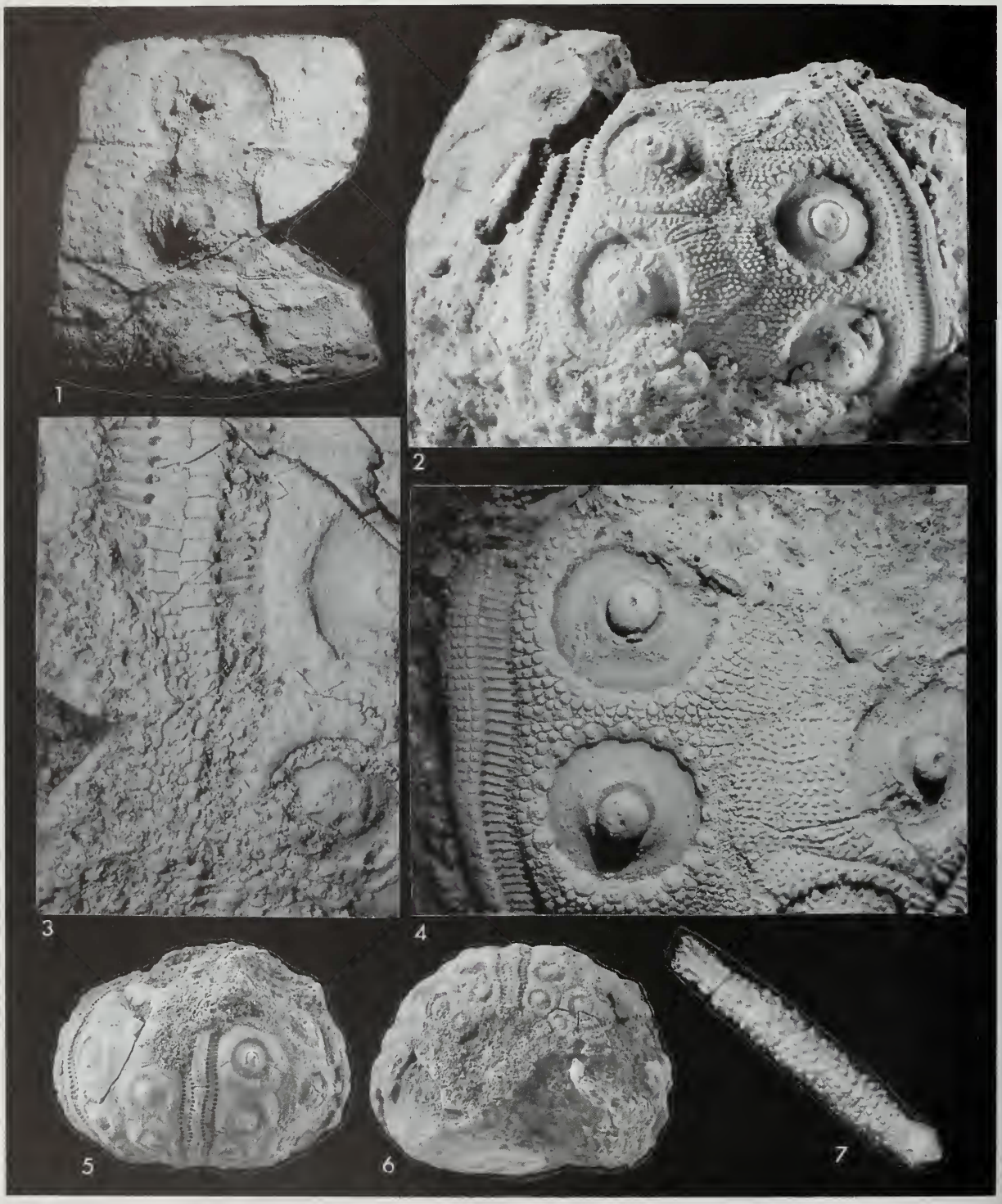


PLATE 1

Fig. 1 Rhabdocidarid gen. et sp. indet. BMNH EE3438; three interambulacral plates, × 3. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation.

Figs 2, 4 *Prionocidaris morgani* (Gauthier). BMNH EE3433. **2**, adapical portion of interambulacrum and adjacent ambulacral zones, × 2·5; **4**, interambulacrum detail, × 4·5. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation.

Figs 3, 5, 6 *Prionocidaris? emiratus* sp. nov. BMNH EE3431, holotype. **3**, ambulacral zone detail, × 10; **5**, lateral, × 2; **6**, oral, × 2. Jebel Huwayyah, section 2, beds 3–6.

Fig. 7 Cidarid spine, possibly belonging to *Prionocidaris morgani* (Gauthier). BMNH EE3434, × 3. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation.

the interradius. There are neural grooves developed in the extra-scrobicular regions.

The smaller specimen (BMNH EE3435) is more complete, but less well preserved. It has seven interambulacral plates in a column at an estimated test diameter of about 35 mm. Adapical interambulacral plates retain fully formed tubercles.

Two cidarid spines were also collected from the scree at Jebel Buhays and probably belong to this species. The best preserved is BMNH EE3434 (Pl. 1, fig. 7). It is 19 mm long by 2·6 mm wide. It has a short neck and a perforate, non-crenulate base. The shaft is widest midlength and tapers towards the tip, but then expands slightly at the very tip to end in a blunt crown. The shaft is covered in rows of thorns which coalesce to form ribs towards the tip.

REMARKS. This species differs from the most common late Cretaceous cidarid described from Iran, '*Cidaris*' *persica* Cotteau & Gauthier (1895), in having much finer and denser extra-scrobicular tuberculation and wider and more strongly conjugate pore-pairs at a comparable size (compare Figs 9A, B). '*C*'. *persica* belongs to the genus *Stereocidaris* and has a characteristic strong interporal ridge developed between pore-pairs. *Cidaris scabra* Gauthier (1902) was established for a 30 mm diameter individual of uncertain provenance within Louristan. It differs primarily in having two ambulacral tubercles to each plate but has very similar strongly conjugate pore-pairs. Ali (1989) described a specimen of *P. morgani* from Jebel Rawdah under the name *Cidaris* cf. *scabra* Gauthier.

Spines comparable in morphology to the one described here have previously been described under the name *Cidaris aftabensis* Gauthier (1902). They can only tentatively be assigned to this species until specimens are found that are attached to a test.

Prionocidaris? emiratus sp. nov. Pl. 1, figs 3, 5, 6; Fig. 9C

TYPE. Holotype and only known specimen, BMNH EE3431.

OCCURRENCE. Found loose in the *Loftusia* levels a little below Beds 6/7, section 2, Jebel Huwayyah.

DIAGNOSIS. A cidarid with conjugate ambulacral pore-pairs and a single primary ambulacral tubercle to each plate, adjacent to the pore-pair. The perradial zone of each ambulacrum is filled with small, dense miliary tuberculation, three or four to a plate and arranged in two rows.

DESCRIPTION. Test 28·5 mm in diameter by 18·9 mm in height. Ambulacra 3·6 mm in width at the ambitus, slightly sinuous. Pore-pairs strongly conjugate, with individual pores of each pair ca. 0·3 mm diameter and separated by an interporal distance of about 0·7 mm (Pl. 1, fig. 3; Fig. 9C). Perradial zone elevated and more or less flat; comparatively short and tall. A large primary tubercle occupies about half of the tuberculate region on each plate (Pl. 1, fig. 5; Fig. 9C). These tubercles are almost contiguous vertically. The central part of the perradial zone is occupied by very much smaller granules, some three or four to a plate, irregularly scattered.

There are six interambulacral plates in a column, of which the most adapical in each zone has only a rudimentary tubercle. Ambital plates are relatively tall and narrow, 7·0 mm wide and 5·8 mm high (Pl. 1, fig. 5). The primary tubercle lies centrally on the plate and has a sunken areole 4 mm in diameter (on ambital plates). The mamelon (1·1 mm in diameter) is perforate and non-crenulate. The surrounding scrobicular circles are non-contiguous. Extra-scrobicular tuberculation is very fine and dense. There are approximately three to four granules abreast on the interradial margin, three abreast adapically and two abreast both adradially and adorally.

REMARKS. The strongly conjugate pore-pairs indicate that this is a member of the Phyllacanthina, and in many respects it is close to *P. morgani* in tuberculation and appearance. The interambulacra are narrower than usual for *Prionocidaris*, and the interradial zones less well developed. Therefore, it is only tentatively assigned to this genus. *P? emiratus* can be easily differentiated from *P. morgani* by its ambulacral tuberculation (compare Figs 9B and 9C). None of the cidarid species described by Cotteau & Gauthier (1895) or Gauthier (1902) have this form of tuberculation.

Indet. cidarid plates

In addition to the specimens described above, fragmentary material of cidaroids has been collected from the basal beds at Jebel Faiyah, section 1, and the *Loftusia* levels (beds 1–6) at Jebel Huwayyah. None of this material is adequate to determine to generic level.

?Order **DIADEMATOIDA** Duncan, 1889
Family **HETERODIADEMATIDAE** Smith & Wright, 1993
Genus ***HETERODIADEMA*** Cotteau, 1864

Heterodiadema buhaysensis sp. nov. Pl. 2, figs 1–3; Figs 10, 11

TYPES. Holotype BMNH EE3441; paratypes, BMNH EE3442–5, EE5019.

OTHER MATERIAL. One other specimen, BMNH EE3446.

OCCURRENCE. Five specimens come from the lowest beds of the Simsima Formation and were collected in the scree derived from the lowest few metres of that formation at Jebel Buhays, section 1. One was collected from the lowest 1·5 m of Simsima Formation at Jebel Thanais. One specimen was collected from bed 5 at Jebel Rawdah, section 3b.

DIAGNOSIS. Apical disc large, pentagonal, caducous; probably monocyclic to judge from the outline. Ambulacra trigeminate, relatively wide with diadematoid-style plate compounding. Phyllodes absent. Primary tubercles perforate, crenulate; reducing in size sharply adapically and tending to become imperforate. Broad zones of granulation along the perradius, adradius and interradius. Peristome invaginated with reasonably deep and sharply defined buccal notches with tags.

DESCRIPTION. Tests range in diameter from 18–36 mm. The test is circular in outline and depressed in profile, with a height 42–48% of the diameter (mean = 45%; Fig. 10). The ambitus lies at about mid-height and the sides are uniformly rounded (Pl. 2, fig. 3). The apical disc and peristome are slightly invaginated in the largest specimen. Coronal plates are all firmly sutured together.

The apical disc is caducous and has been lost from all specimens. The apical disc opening is pentagonal in outline with the angles projecting reasonably strongly into the interradii (slightly more into the posterior interradius, which isalso

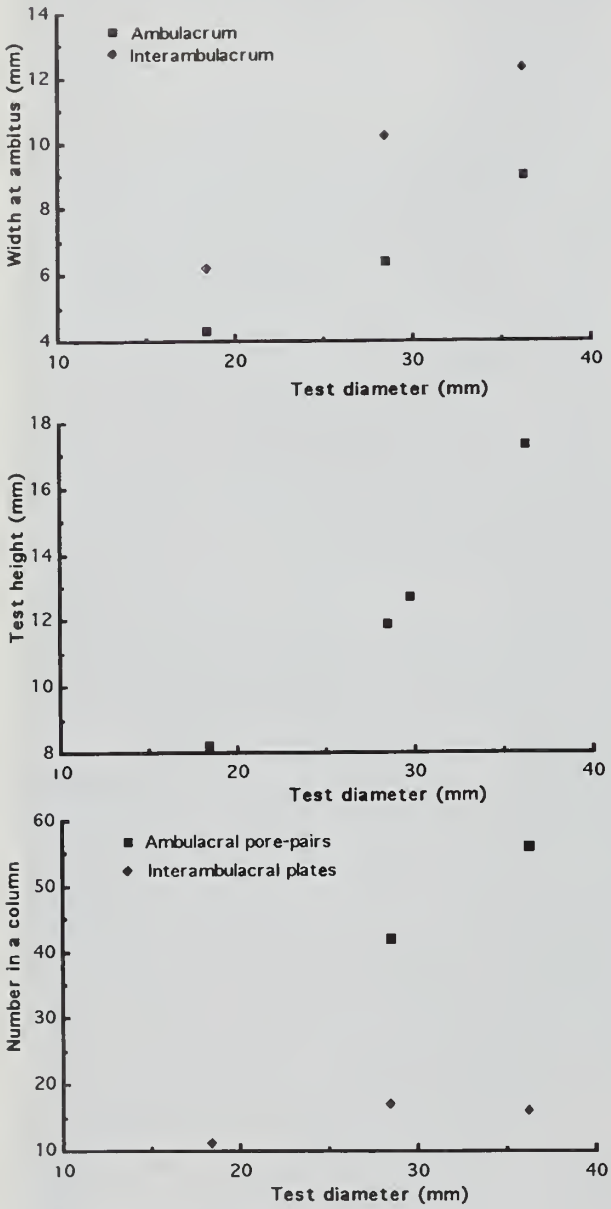


Fig. 10 Biometric data for *Heterodiadema buhaysensis* sp. nov.

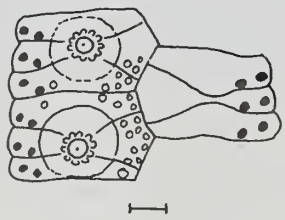


Fig. 11 Camera lucida drawing of three ambital ambulacral plates of *Heterodiadema buhaysensis* sp. nov., BMNH EE3444. Scale bar = 1 mm.

more rounded). It is a little longer than broad with a length that is 36–43% of the test length.

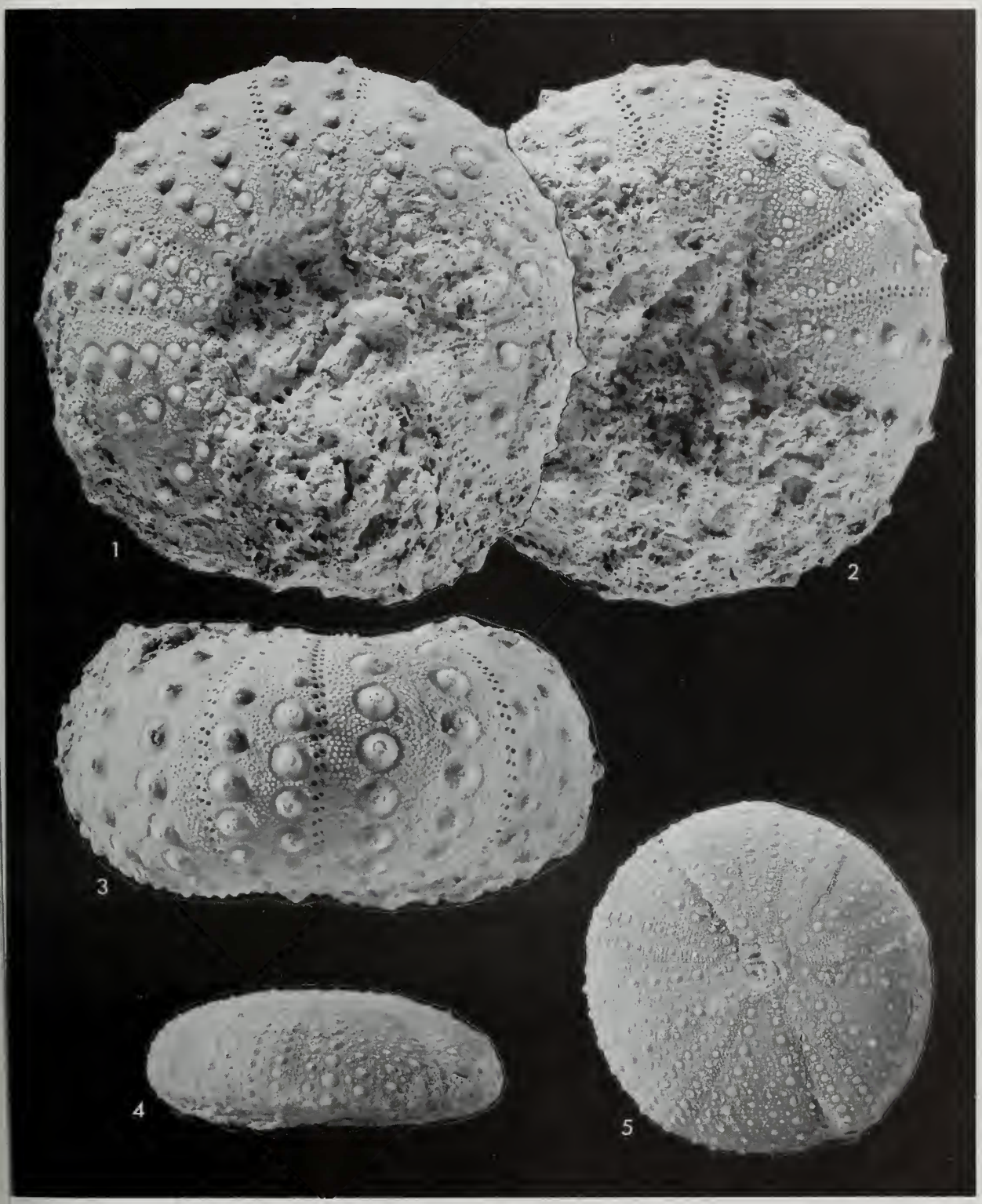
Ambulacra are broad and nearly parallel-sided at the ambitus but taper gradually both adapically and adorally. At the ambitus they have a width that is 23–25% of the test length. Pore-pairs are uniserial throughout, without any widening whatsoever at the peristomial margin. Plates are compound, with diadematoid-style triads in which the central element is the largest and upper and lower elements both taper towards the perradial and adradial suture (Fig. 11). Each triad bears a primary tubercle and there is a well-developed perradial band of miliary tuberculation that expands adapically. At the ambitus in the largest specimen perradial tubercles are about three abreast. Oral and ambital tubercles are perforate and crenulate, but tubercles reduce sharply in size above the ambitus, where they may become imperforate and non-crenulate (some remain perforate). This reduction in size occurs above about the seventh compound plate. Larger tubercles have circular, non-confluent areoles. At the ambitus pore-pairs are rather widely spaced and separated by a single row of miliary tubercles. There are no obvious sphaeridial pits around the peristome.

Interambulacra are about 1·3–1·5 times as wide as the ambulacra. There are 15 plates in a column at 36 mm test diameter. All plates have a single large primary tubercle that is perforate and crenulate and is surrounded by a circular areole. The mamelon is notable for its small size in comparison to the size of the areole. Areoles are non-confluent, being separated for the most part by a single band of miliaries. Tubercles decrease in size sharply towards the apex and may become imperforate. There are broad zones of uniform miliary tuberculation both adradially and interradially: about six abreast adradially and three or four abreast interradially at the ambitus in the largest specimen. Scrobicular tubercles are not differentiated.

The peristome is relatively large, 28% of test diameter in a 36 mm diameter individual. It is strongly indented by the buccal notches. There are broad, smooth tongue-like regions running adradially from each buccal notch and extending up to the fourth interambulacral plate.

Remarks. This species is most closely related to the mid-Cretaceous (Cenomanian) *Heterodiadema lybica* (Agassiz & Desor). Both have a similar form of ambulacral compounding and a very similar tuberculation style. Granular zones are broad and well developed and in both there is a sharp reduction in the size of primary tubercles above the ambitus, with those adapically tending to become imperforate and non-crenulate. Finally, both have the distinctive tubercle-free tag to the buccal notches and uniserial pore-pairs throughout. *H. buhaysensis* differs from *H. lybica* in having fewer reduced tubercles, the primary tubercles becoming smaller considerably closer to the apex in *H. buhaysensis* in individuals of comparable size. It also differs in lacking the extreme prolongation of the apical disc into the posterior interambulacrum seen in medium to large specimens of *H. lybica*.

Heterodiadema was placed in its own family by Smith & Wright (1993). Where this family fits into the higher taxonomy of echinoids, however, is much less certain. They may be members of the aulodont group Diadematoida. This is suggested by the prominent buccal tags and the very delicate mamelons on the primary tubercles, which indicate that the species had small, fragile spines. Alternatively they may be stirodonts, early members of the Phymosomatoida (as



ATE 2

s 1–3 *Heterodiadema buhaysensis* sp. nov. BMNH EE3441, holotype; **1**, oral; **2**, apical; **3**, lateral; all × 3. Jebel Buhays, section 1; loose n the scree derived from the lowest 3 m of the Simsima Formation.

s 4, 5 *Orthopsis miliaris* (d'Archiac). Topotype specimen of *Orthopsis morgani* Cotteau & Gauthier, from the Morgan Collection, Museum d'Histoire Naturelle, Paris, × 2. Senonian, Khianan, Iran.

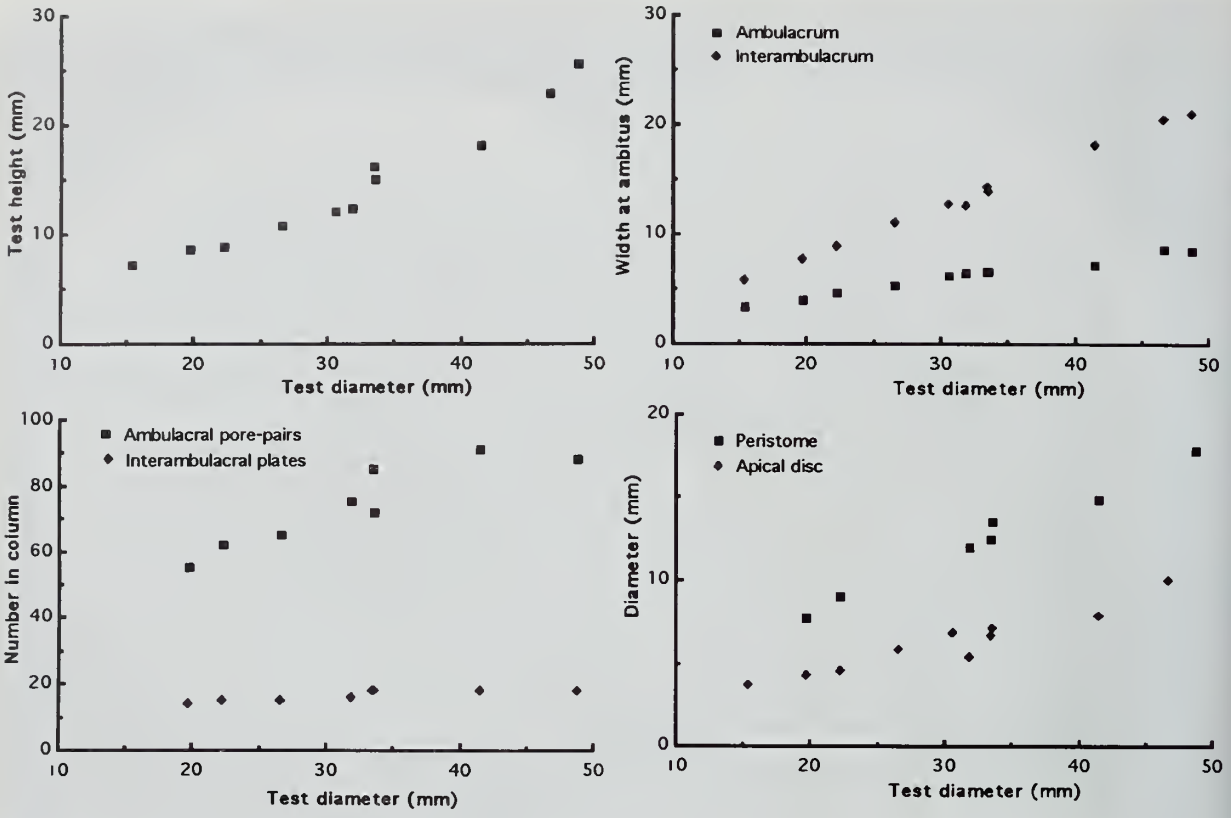


Fig. 12 Biometric data for *Orthopsis miliaris* (d'Archiac).

defined by Smith & Wright, 1993). Diadematoids and phymosomatoids are fundamentally differentiated on the structure of their spines and lantern apparatus, diadematoids having hollow spines and grooved teeth, phymosomatoids having solid spines and keeled teeth. In neither *H. lybica* nor in our new species are the spines or lantern known, thus its higher taxonomic position must remain unresolved. Because of its delicate tuberculation, it is tentatively assigned here to the Diadematoida.

Infraclass **ACROECHINOIDEA** Smith, 1984
Plesion (Order) **ORTHOPSIDA** Mortensen, 1942
Family **ORTHOPSIDAE** Duncan, 1889
Genus ***ORTHOPSIS*** Cotteau, 1864

Orthopsis miliaris (d'Archiac, 1835) Pl. 2, figs 4, 5; Pl. 3, figs 1–9; Figs 12–14

1835 *Cidarites miliaris* d'Archiac: 179, pl. 11, fig. 8.
1895 *Orthopsis morgani* Cotteau & Gauthier: 87, pl. 14, figs 6–9.
1933 *Orthopsis sanfilippoi* Checchia-Rispoli: 6, pl. 1, figs 5–15.
1985 *Orthopsis miliaris* (d'Archiac); Geys: 143, pl. 5, figs 8–10 (see also for full prior synonymy).
1989 *Orthopsis morgani* Cotteau & Gauthier; Ali: 401, fig. 2 (7).
1991 *Orthopsis miliaris* (d'Archiac); Smith & Bengtson: 30, pl. 8B-F, text-fig. 23.

MATERIAL STUDIED. Forty seven specimens of which the following 11 were used in the biometric analysis: BMNH EE3720–21, EE3723, EE3725–26, EE3728, EE3731, EE3733, EE3738, EE3740, EE3749 and EE5018.

OCCURRENCE. In the western Oman mountains this species occurs at the following localities and horizons (numbers in brackets are number of specimens):
Jebel Buhays, section 1: loose in scree derived from lowest few metres of the Simsima Formation (13)
Jebel Thanais: lowest 2 m of Simsima Formation (1).
Jebel Huwayyah, section 2: Loftusia levels (beds 3–5; 1 fragment).
Jebel Rawdah, section 1: beds 3 and 4, and loose (4).
Jebel Rawdah, section 3b: bed 2 (1); bed 3, 1m above base (1), bed 8 (2); bed 9 (8); bed 10 (1); loose (3).
Jebel Rawdah section 4: bed 12 (5);top of bed 15 (1); loose, lower half of sandy beds (1).
Jebel Faiyah, section 1a: top of bed 2 (1).

DESCRIPTION. Tests range from 20 mm to 48 mm in diameter and are circular in outline and bun-shaped in profile. Test height is 39–52% of test diameter (Fig. 12) and in profile the ambitus lies about one third the height above the base.

The apical disc is dicyclic, though occasionally one of the posterior oculars may just be exsert. The apical disc occupies 17–24% of the test diameter (mean = 21%, SD = 1·9%, N = 10; Fig. 12). Genital plates are broad and crescentic in outline, except for the madreporite, which is larger and more pentagonal in outline (Pl. 3, fig. 7; Fig. 13A). Madrepores occupy almost the entire surface of the madreporite plate and

there are small scattered tubercles amongst the openings. Gonopores are present even in the 20 mm diameter individual. Ocular plates are small and pentagonal. All plates have small secondary tubercles, those on the genital plates tending to form a circle around the periproct. The periproct is irregularly oval in outline and occupies 10–14% of the test diameter.

Ambulacra are 17–21% of the test diameter in width at the ambitus (mean = 20%, SD = 1·3%, N = 11). Plating is trigeminate throughout and pore-pairs are arranged either uniserially or in very weak arcs of three (Pl. 3, fig. 6). All ambulacral elements are narrow and elongate and reach the perradius (Fig. 13B). A primary tubercle (perforate and non-crenulate) straddles two of the three elements in each compound plate (Pl. 3, fig. 6). The third element carries two small secondary tubercles and an intermediate row of miliary granules. There are secondary and miliary tubercles down the perradius also. Adorally only the first five or so pore-pairs are offset to form a weak phyllode (Fig. 13C). There are 55 pore-pairs in a column at 20 mm test diameter, rising to around 90 at 46-48 mm diameter (Fig. 12). Sphaeridial pits are very shallow and are present on the two or three most adoral compound plates, immediately adjacent (perradial) to the pore-pair on the element in each triad that does not support a primary tubercle.

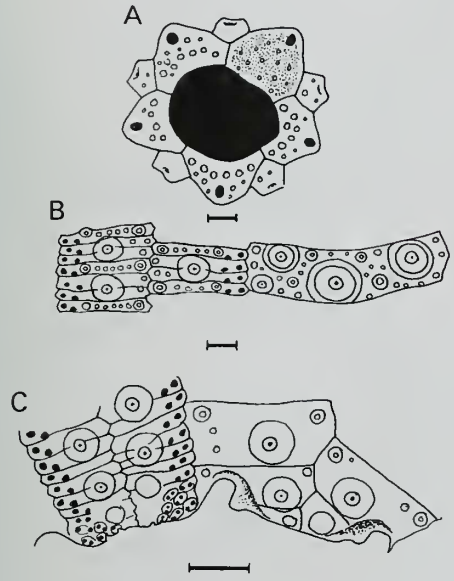


Fig. 13 Camera lucida drawings of plating in *Orthopsis miliaris* (d'Archiac). **A**, apical disc plating, BMNH EE3723; **B**, ambital ambulacral (left) and interambulacral (right) plates, BMNH EE3723; **C**, adoral plating, ambulacrum to left, interambulacrum to right, BMNH EE3733. Scale bars: A, B = 1 mm; C = 2 mm.

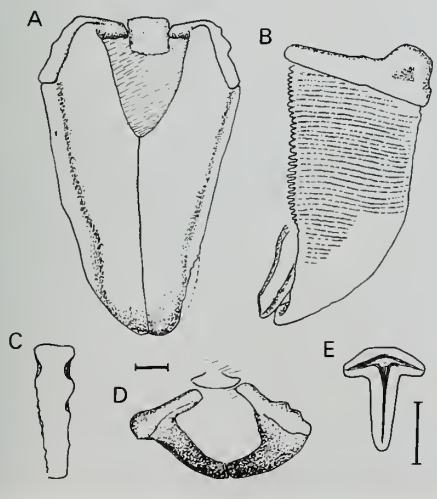


Fig. 14 Camera lucida drawings of lantern elements in *Orthopsis miliaris* (d'Archiac): A-D, BMNH EE3735; E, BMNH EE5020. **A**, pyramid with rotula and tooth in position; **B**, same in lateral view; **C**, fragment of compass element; **D**, adapical view of pyramid, with proximal end of tooth (broken) towards the top; **E**, cross-section of a single tooth. Scale bars = 1 mm.

Interambulacra are 38–44% of the test diameter in width at the ambitus (mean = 41%, SD = 2·0%, N = 11) (Fig. 12). Ambital plates are short and wide and slightly curved. At the ambitus most specimens have a single primary tubercle, centrally positioned, plus two smaller secondary tubercles one on either side (Pl. 3, figs 3, 8; Fig. 13B). However, in a fragment of a large specimen (*ca.* 65 mm diameter, BMNH EE3717), there is a fourth large tubercle on the interradial margin. The remainder of the plate carries scattered tertiary tubercles and granules. All tubercles are perforate and non-crenulate. Adorally there is no primordial plate. There are 14 plates in a column at 20 mm test diameter, rising to 18 at 42–48 mm test diameter (Fig. 12).

The peristome is 36–40% of the test diameter in diameter (mean = 38%, SD = 1·7%, N = 7). It is slightly invaginated. There are strong buccal notches that extend into the second interambulacral plate (Pl. 3, fig. 9; Fig. 13C).

The perignathic girdle is seen in BMNH EE3733. The auricles are well developed. They meet and are fused above the perradius to form a continuous arch.

Lantern elements are preserved within the tests of several specimens, but are best seen in BMNH EE3735. Hemipyramids are tall and have a relatively shallow foramen magnum, only some 33% of their height (Figs 14A, B). There is a clear muscle attachment flange on the outer edge of each. The upper surface of the lantern is also pitted. There are well-developed processus superalveolares that extend to the tooth. The lateral (inter-pyramidal) face is denticulate along its inner edge and has the usual horizontal series of ridges for muscle attachment.

The epiphyses are not clearly seen in any specimen but appear relatively short. They are definitely not extended above the foramen magnum nor are they fused together as is the case in camarodont lanterns. There is a single compass element that is slender and has a small head (Fig. 14C). The tooth is strongly keeled and is best seen in cross section in BMNH EE5020 (Fig. 14E).

Spines are seen associated with lantern elements in BMNH EE3735. They are relatively short and needle-like, with a small base and no cortex. The spines are solid, not hollow.

Remarks. The lantern of *Orthopsis* was described from late Cretaceous specimens of *O. sanfilippoi* Checchia-Rispoli (here treated as a synonym) by Serra (1934), who gave only a sketchy illustration of the apparatus, but pointed out its keeled teeth. Serra, and later Mortensen (1943: 11) described the latern as camarodont. However, this is clearly not the case since the epiphyses are not fused together to form a brace for the tooth. Instead both the hemipyramid and the

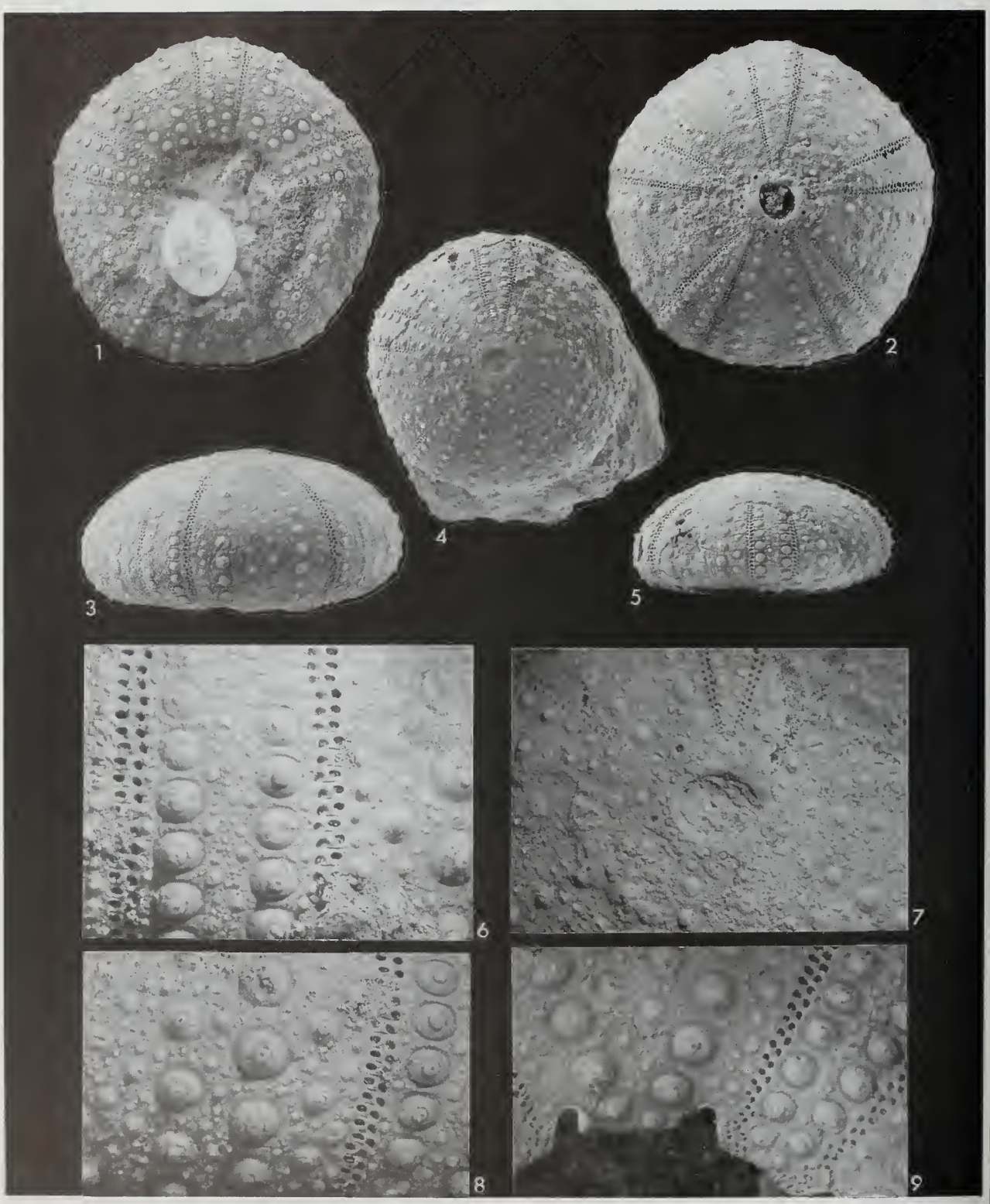


PLATE 3

Figs 1–9 *Orthopsis miliaris* (d'Archiac). **1–3**, BMNH EE3740; **1**, oral; **2**, apical; **3**, lateral; all × 2. Jebel Rawdah, section 3, bed 9. **4, 5, 7**, BMNH EE3725; **4**, apical, × 2; **5**, lateral, × 2; **7**, apical disc, × 4. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation. **6, 8, 9**, BMNH EE3733; **6**, ambital ambulacrum, × 6; **8**, ambital interambulacrum, × 6; **9**, peristomial region, × 6. Jebel Rawdah, section 1, bed 3.

epiphysis extend adaxially towards the tooth as in diadematoid and stirodont lanterns (Jensen 1981, figs 31, 32). The epiphyses are well-separated and although they may actually reach the tooth and support it, they remain far apart. The tooth is undoubtedly keeled and similar to those of stirodonts and camarodonts.

The phylogenetic position of orthopsids can now be clarified. The structure of their epiphyses and hemipyramids is primitive for euechinoids as a whole, thus there are no grounds for treating orthopsids as camarodonts. The keeled teeth and solid spines place orthopsids as acroechinoids and more derived than either diadematoids or echinothurioids. However, the simple acrosaleniid-style of ambulacral plate compounding and the perforate, non-crenulate nature of the primary tubercles differentiate it from all other acroechinoids. They are best considered as an early plesion of the Acroechinoidea.

Orthopsis morgani Cotteau & Gauthier (1895), from the late Senonian of southern Iran (Pl. 2, figs 4, 5) is treated as a synonym.

Order **CALYCINA** Gregory, 1900
Family **SALENIIDAE** Agassiz, 1838
Genus *SALENIA* Gray, 1835

Salenia nutrix Peron & Gauthier, 1881 Pl. 4, figs 1–13; Pl. 17, figs 4, 5; Figs 15, 16A–E, G, H

1881 *Salenia nutrix* Peron & Gauthier, in Cotteau, Peron & Gauthier: 167, pl. 18, figs 4–10.
1895 *Salenia cossiaea* Cotteau & Gauthier: 83, pl. 13, figs 13–19.
1902 *Salenia cossiaea* Cotteau & Gauthier; Gauthier: 149, pl. 18, fig. 12.
1928 *Salenia cossiaea* Cotteau & Gauthier; Lees: 659.
1932 *Salenia lamberti* Checchia-Rispoli: 6, pl. 2, figs 1–5.
1969 *Salenia geometrica* Agassiz; Devries: 167, pl. 1, fig. 1, pl. 4, figs 1–3.
1989 *Salenia cossiaea* Cotteau & Gauthier; Ali: 398, fig. 2.6.

MATERIAL. 34 specimens, BMNH EE3622–EE3654, EE3656.

OCCURRENCE. In the western Oman Mountian sections studied this species was found as follows:
Jebel Aqabah; lowest few metres of the Simsima Formation (2).
Jebel Buhays, section 1; loose in scree derived from lowest few metres of the Simsima Formation (7).
Jebel Buhays, section 3: loose in scree (2).
Jebel Faiyah, section 1: bed 8 (2).
Jebel Rawdah, section 1; beds 3 and 4 (4); loose in scree (1).
Jebel Rawdah, section 2; beds 6–8 (10); bed 11 (2); bed 13 (2); loose in scree (3).
Jebel Rawdah section 3; bed 2b (1); bed 10 (1).
Jebel Rawdah section 4; bed 10 (1).

This species also occurs in the Upper Campanian of Nafun, 3·5 km west of Surayr, near Dumq, Oman (Skelton *et al.* 1990). It was originally described from the 'Etage dordonien inferieur, couches a *Heterolampas maresi*' (Late Campanian or early Maastrichtian) of Algeria. Later Gauthier (1902) described the same species from the Campanian of Tunisia. Cotteau & Gauthier described a very similar form from the Senonian of Persia (Iran) under the name *Salenia cossiaea* (Pl. 4, figs 4–6). Finally, Devries (1967) described this species from Turkey under the name *Salenia geometrica* Agassiz.

DIAGNOSIS. Rather inflated species of *Salenia* with seven to eight interambulacral plates at test diameters of 23–28 mm. Apical disc relatively small, circular and flat with periproct and suranal equal in size. Ocular I insert or exsert. Numerous small pits developed along all apical disc sutures in larger specimens, but largest along genital/ocular plate boundaries. Interradial granular zone well developed in specimens greater than 23 mm test diameter.

DESCRIPTION. Tests range in diameter from 7 to 26 mm. Test height in specimens larger than about 10 mm is 60–76% of the diameter (mean 65%, N = 19; Fig. 15). The test is thus rather inflated in profile and in some specimens almost subglobular (Pl. 4, fig. 3).

The apical disc is rather flat and only rises very slightly towards the apex. Its diameter is 42–55% of the test diameter (mean = 46%, N = 19). It is subcircular in outline. The suranal plate is relatively large, on average about 25% of the apical disc diameter. It is similar in size to the genital plates. The periproct is approximately the same size as the suranal plate, or very slightly larger, being on average 27% of the apical disc diameter. In some specimens ocular 1 is strongly exsert and forms the posterior wall of the periproct, but in other specimens ocular 1 is insert and separated from the periproct (Figs 16A-E). Approximately half of the specimens have the ocular plate insert. There is a slight elevation towards the periproct edge, but no true rim is developed. All plates are smooth and unornamented. The sutures are usually incised and may have a series of small pits along their length (Pl. 4, figs 1, 4, 7, 11). The ocular/genital plate boundaries always have pits that are more prominent than the rest. Gonopores are present on genital plates from approximately 10 mm diameter.

Ambulacra are narrow and only very slightly sinuous towards the apex (Pl. 4, fig. 13). They expand adorally to form a short phyllode. Plating is strictly bigeminate throughout. There are 45 pore-pairs in a column at 13 mm test diameter, rising to 78 at 26 mm test diameter (Fig. 15). Each compound plate has a primary tubercle that forms a contiguous row adjacent to the pore-pairs (Figs 16G, H). The perradial zone is narrow, but there is a single secondary tubercle on each compound plate and a single zig-zag row of miliaries also. On the oral surface up to 12 pore-pairs become crowded into a short phyllode in the largest specimens. There are approximately 15 or 16 ambulacral plates opposite an ambital interambulacral plate in individuals of 20–26 mm test diameter.

Interambulacra remain relatively broad throughout. There are six interambulacral plates in a column from 10–16 mm test diameter, rising to eight by about 25 mm diameter (Fig. 15). Plates at the ambitus are slightly wider than tall and the primary tubercle lies towards the adradial margin, leaving a relatively broad interradial zone in specimens larger than about 22 mm diameter. Primary tubercles are imperforate and crenulate and are surrounded by five or six secondary tubercles (non-contiguous) (Pl. 4, fig. 13). The interradial zone has miliary tubercles from about 15 mm test diameter upwards and in larger specimens this forms a broad and distinctive band that runs almost to the peristome edge.

The peristome is on average 48% of the test diameter

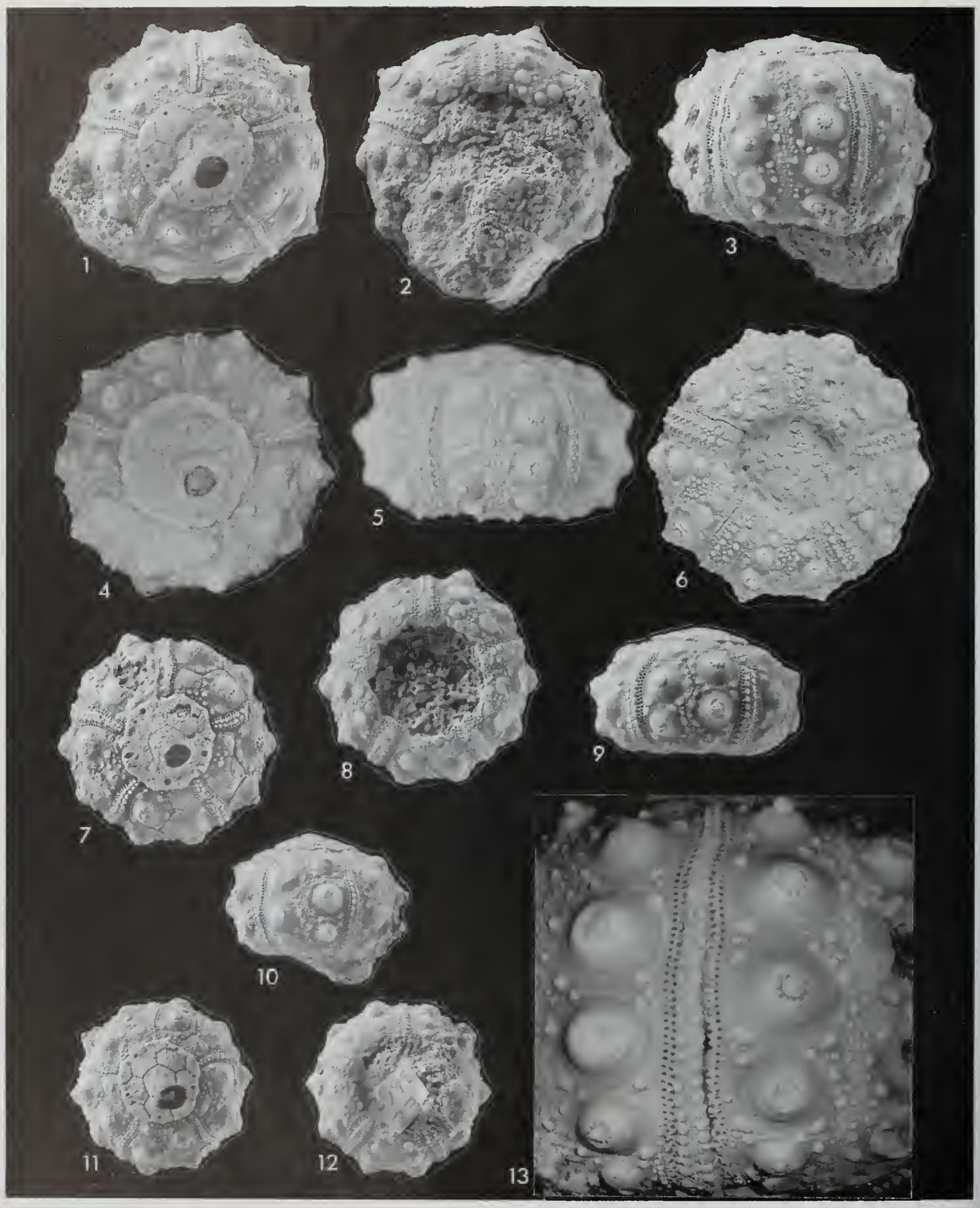


PLATE 4

Figs 1–13 *Salenia nutrix* Peron & Gauthier. **1–3, 13**, BMNH EE3646; **1**, apical, × 2; **2**, oral, × 2; **3**, lateral, × 2; **13**, ambital detail, × 5. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation. **4–6**, B18723a, Museum d'Histoire Naturelle, Paris; topotype material from the Morgan Collection of *Salenia cossiae* Cotteau & Gauthier; **4**, apical; **5**, lateral; **6**, oral; all × 3. Senonian, Kala é Melek, Iran. **7–9**, BMNH EE3651; **7**, apical; **8**, oral; **9**, lateral; all × 2. Jebel Buhays, lowest 2 m of the Simsima Formation. **10–12**, BMNH EE3652; **10**, lateral; **11**, apical; **12**, oral; all × 2. Jebel Buhays, lowest 2 m of the Simsima Formation.

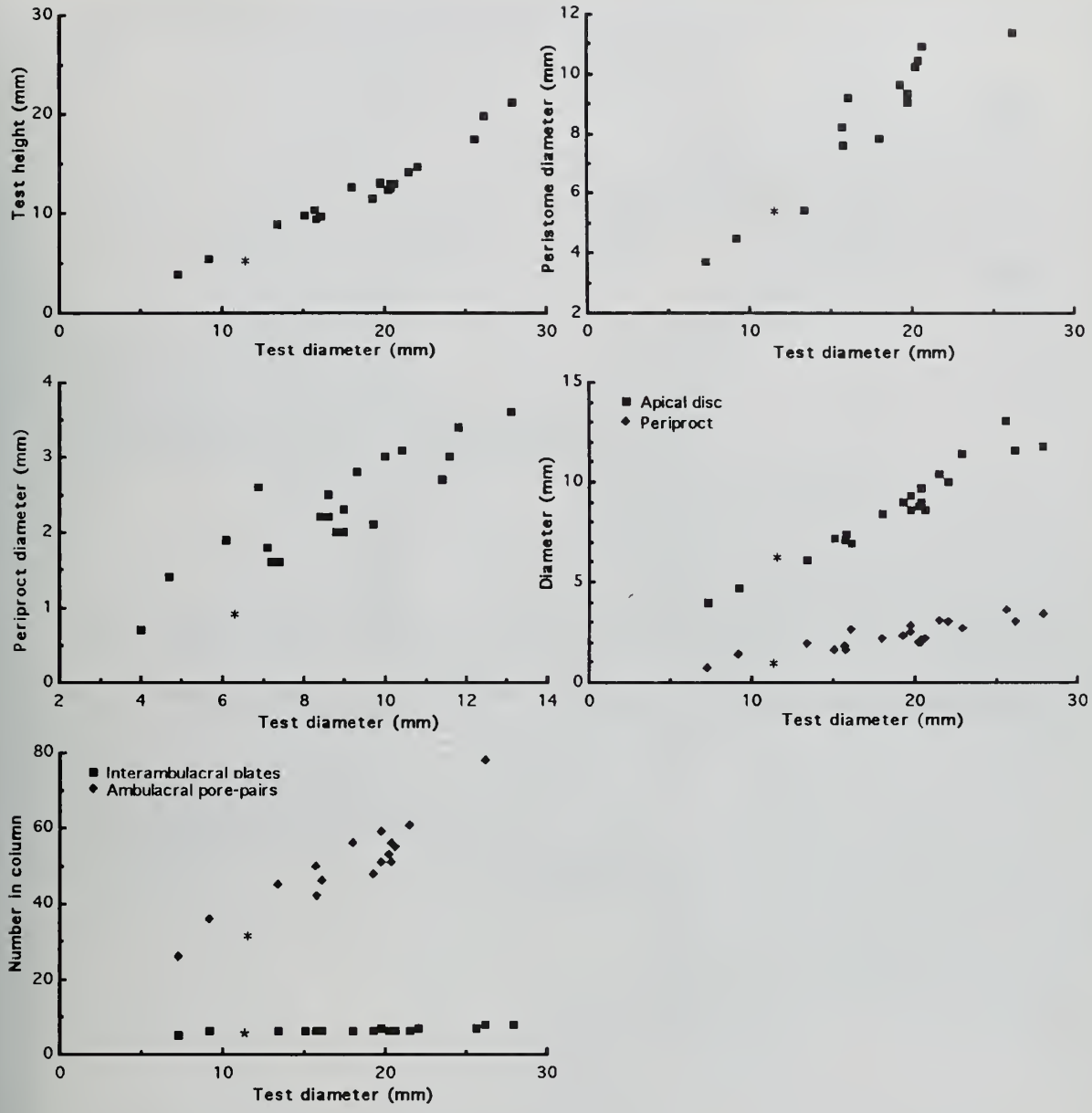


Fig. 15 Biometric data for *Salenia nutrix* Peron & Gauthier (squares) and *S. microprocta* sp. nov. (crosses).

across. It is hardly invaginated and has feeble buccal notches (Pl. 4, figs 2, 6, 8, 12).

Remarks. This species somewhat resembles *S. geometrica* Agassiz, but differs from that species in having a relatively smaller apical disc and a larger periproctal opening. It also has much less pronounced pits developed at triple suture junctions on the apical disc. Although there are clearly two morphological forms, those with ocular 1 insert and those with ocular 1 exsert, the apical discs are in all other respects identical and the two forms co-occur in the various sections. I therefore treat the two forms as variants of the same species. The form described by Checchia-Rispoli (1932*a*) as *S. lamberti* from the Maastrichtian of Libya has all the characteristics of *S. nutrix*, except that ocular 1 is reportedly always insert. It too is treated as part of this same species complex. *S. nutrix* resembles *S. loveni* (Cotteau) in having a rather flat and smooth apical disc and in having expanded phyllodes adorally. However, it is very different both in the relative size of the apical disc (which in *S. loveni* occupies most of the upper surface) and in the coarseness of the tuberculation. *S. maxima* Arnaud and *S. belgica* Lambert are also similar in having fine sutural pitting but also have relatively much larger apical discs than is seen in *S. nutrix*.

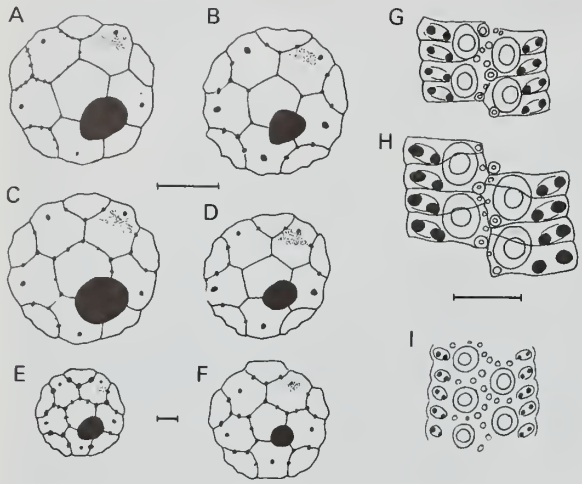


Fig. 16 Camera lucida drawings of plating in *Salenia*. **A-E**, apical discs of *Salenia nutrix* Peron & Gauthier; A, BMNH EE3646; B, BMNH EE3654; C, BMNH EE3647; D, BMNH EE3651; E, BMNH EE3627. **F**, apical disc of *Salenia microprocta* sp. nov. BMNH EE3657. **G, H** ambital ambulacral plating of *Salenia nutrix* Peron & Gauthier; G, BMNH EE3647; H, BMNH EE3638. **I**, ambital ambulacral plating of *Salenia microprocta* sp. nov., BMNH EE3657. Scale bars; A-D = 5 mm; E, F = 1 mm; G-I = 1 mm.

Salenia microprocta sp. nov Pl. 5, figs 13; Figs 15, 16F, I

TYPE. Holotype and only known specimen, BMNH EE3657.

OCCURRENCE. Jebel Huwayyah, section 2: bed 1.

DIAGNOSIS. A small, flattish *Salenia* with a relatively large, flat, pentagonal apical disc and a small oval periproct. Ambulacral tubercles are not contiguous and at the ambitus may be separated by granules.

DESCRIPTION. Test 11·4 mm in diameter and 5·1 mm in height (45% of test diameter). Depressed in profile with a broad flat base and top. The ambitus is uniformly rounded. The apical disc is flat and pentagonal in outline, with the angles radial. The disc is 55% of the test diameter in length. The genital plates are approximately as broad as long and are all similar in size (Fig. 16F). Ocular plates protrude slightly. The suranal plate is relatively large, whereas the periproct is small (Pl. 5, fig. 1), being only 17% of the apical disc diameter along the plane of bilateral symmetry. There is no lip to the periproct. Sutural pits are present at all plate triple junctions and also mid-way between these junctions. Small gonopores are present.

The ambulacra are slightly sinuous adapically, becoming straight adorally and expanding towards the peristome. There are 33 pore-pairs in a column and 16 primary tubercles. All plates are compound and bigeminate. At the ambitus the ambulacral width is 1·5 mm with the perradial tuberculate zone making up 1·0 mm of this width. Primary tubercles are relatively small and are not contiguous with their neighbours. There is a single row of miliary tubercles perradially and, at the ambitus, there is also a single row of miliaries between successive primary tubercles (Pl. 5, fig. 3; Fig. 16I). Small phyllodes are developed adorally.

Interambulacra are composed of five plates in each column. Each has a single primary tubercle surrounded by six widely-spaced scrobicular tubercles. There is a single row of miliary tubercles down the interradius.

The peristome is very slightly invaginated and is 50% of the test diameter in diameter. There are feeble buccal notches.

REMARKS. No other *Salenia* species has ambulacra with primary tubercles separated by rows of granules. *S. microprocta* is also easily distinguished from small specimens of *S. nutrix* by the very small size of its periproct and the relatively large area occupied by the apical disc.

Order **ARBACIOIDA** Gregory, 1900
Family **GONIOPYGIDAE** Smith & Wright, 1993
Genus ***GONIOPYGUS*** Agassiz, 1838

Goniopygus arabicus sp. nov. Pl. 6, figs 3–10; Pl. 7, figs 1, 3, 5, 6; Figs 17, 18A, B, D, E, G

1972 *Goniopygus superbus* Cotteau & Gauthier; Kier: 68, pl. 42, figs 1–3.
1989 *Goniopygus superbus* Cotteau & Gauthier; Ali: 401, fig. 2 (2).

TYPES. The holotype is BMNH EE4012, paratypes are BMNH EE3983–84, EE39896, EE3992, EE3997, EE4005, EE4007, EE4015, EE4017 and EE4019.

MATERIAL STUDIED. Forty-four specimens of which the type series was used in the biometric analysis.

OCCURRENCE. In the western Oman Mountains this species is found at the following levels:
Jebel Buhays, section 1: loose in scree derived from the lowest few metres of the Simsima Formation (29): bed 12 (1).
Jebel Buhays, section 2: loose in scree derived from the basal few metres of the Simsima Formation (4).
Jebel Buhays, section 3: basal 1 m of the Simsima Formation (4).
Jebel Thanais: lowest 1 m of the Simsima Formation (2).
Jebel Faiyah, section 1: bed 6 (1 fragment).
Jebel Rawdah, section 2: bed 4 (1): beds 6–8 (10); bed 10 (1); bed 11 (1).
Jebel Rawdah, section 3a, bed 2 (2).

Elsewhere the species has been reported from the late Campanian of the Rihyad district of Saudi Arabia (Kier 1972).

DIAGNOSIS. A species of *Goniopygus* with relatively narrow ambulacra with a single small secondary tubercle on each compound plate, a trigonal periproct with, predominantly, three perianal tubercles and apical disc plating that is smooth and unornamented. Gonopores lie on the genital plates.

DESCRIPTION. Tests range in size from 25 to 41 mm in diameter and are circular in outline. Test height is 53–62% of test diameter (mean = 57%, SD = 3·0%, N = 9: Fig. 17). Both the base and top are flat in profile and the ambitus lies at approximately mid-height (Pl. 6, figs 4, 5, 7). The apical disc plates are elevated above the corona.

The apical disc is flat, large and prominent. It occupies 35-43% of the test diameter (mean = 40%, SD = 3·3%, N = 9). Genital plates are pointed distally and the gonopore opens

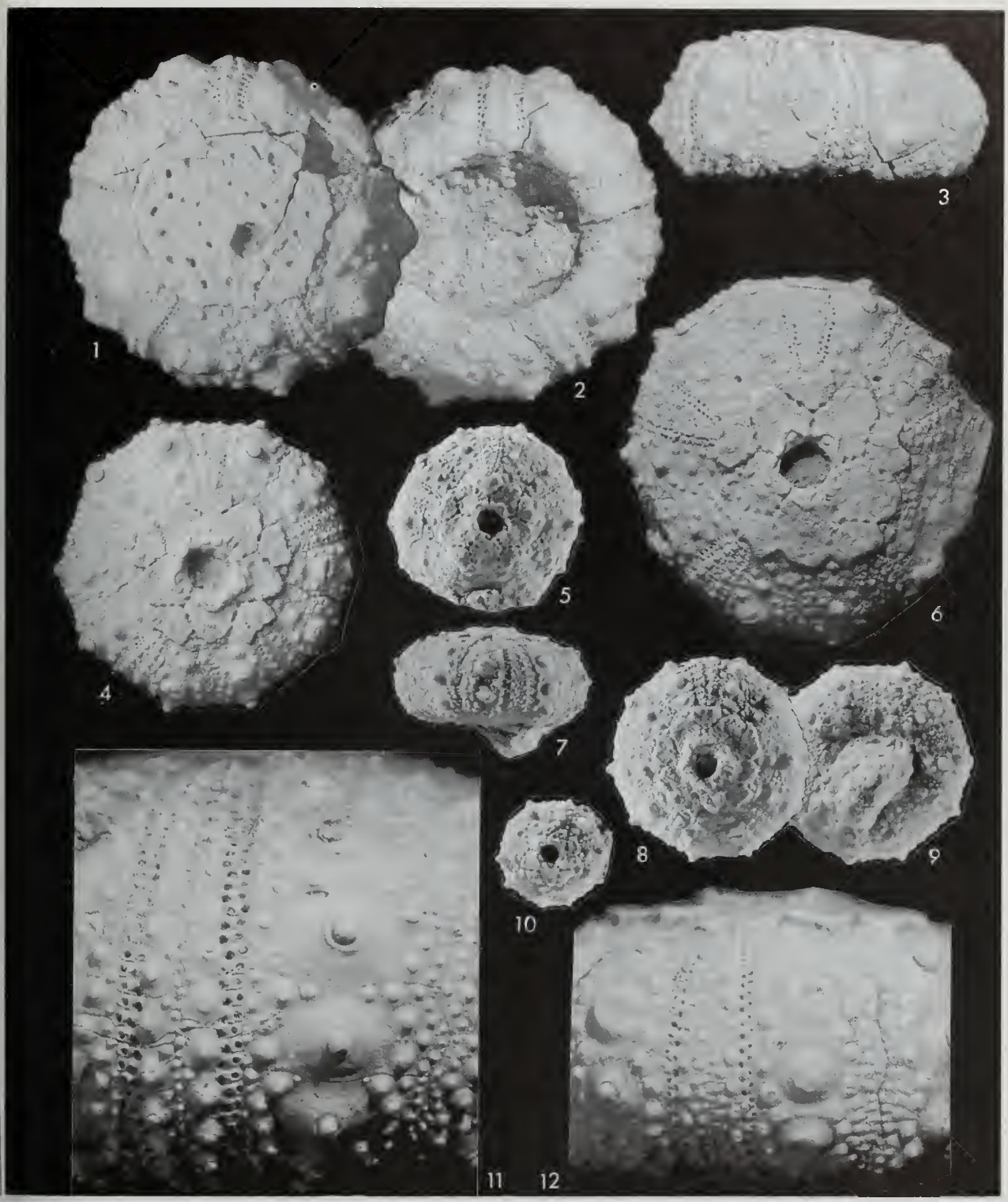


PLATE 5

Figs 1–3 *Salenia microprocta* sp. nov. BMNH EE3657, holotype; **1**, apical; **2**, oral; **3**, lateral; all × 6. Jebel Huwayyah, section 2, bed 1.

Figs 4–10, 12 *Mimiosalenia quinquetuberculata* gen. et sp. nov. Jebel Faiyah, section 1, bed 7. **4, 12,** BMNH EE3981, holotype; **4**, apical, × 4; **12**, lateral, ambulacrum detail, × 8. **5, 6,** BMNH EE3982, paratype, apical; **5**, × 3; **6**, × 6. **7–9**, BMNH EE3978, paratype; **7**, lateral; **8**, apical; **9**, oral; all × 3. **10**, BMNH EE3980, paratype; apical, × 3.

Fig. 11 *Glyphopneustes hattaensis* Ali. BMNH EE4027, detail of ambital region, lateral view, × 8; Jebel Thanais, lowest 2 m of the Simsima Formation.

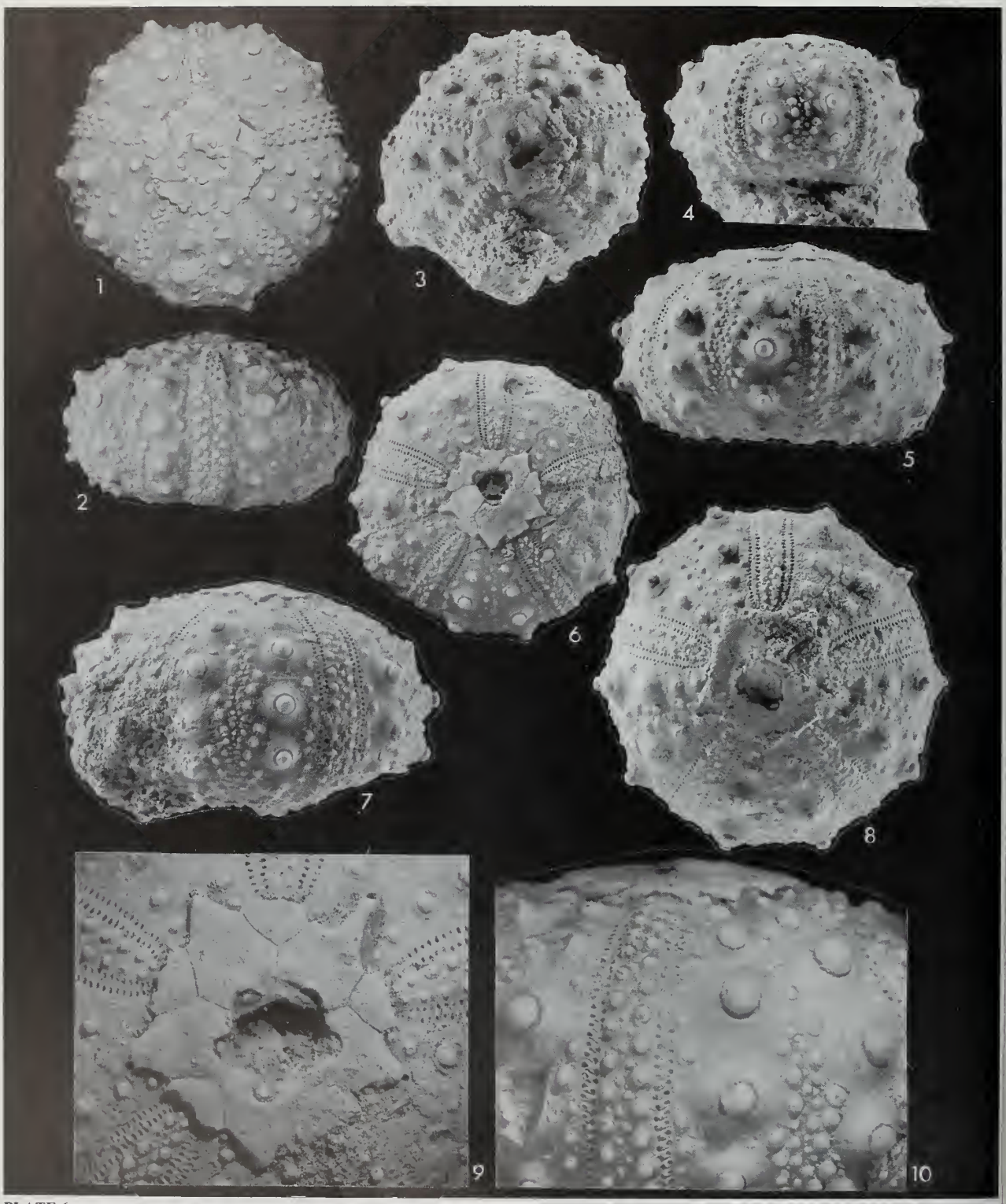


PLATE 6

Figs 1, 2 *Goniopygus superbus* Cotteau & Gauthier. L12680, Lambert Collection, Geology Department, Université de Paris VI, Paris; **1**, apical; **2**, lateral; both × 2. Senonian, Derré-i-Chahr, Iran.

Figs 3–10 *Goniopygus arabicus* sp. nov. **3, 4, 10** BMNH EE4005, paratype; **3**, apical; **4**, lateral; both × 2; **10**, ambital detail, × 5. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation. **5, 8**, BMNH EE4017, paratype; **5**, lateral; **8**, apical; both × 2. Jebel Rawdah, section 2, bed 6. **6, 7**, BMNH EE4012, holotype; **6**, apical, × 1·6; **7**, lateral, × 2. Jebel Rawdah, section 3, bed 2. **9**, BMNH EE3983; apical disc, variety with five perianal tubercles, × 5. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation.

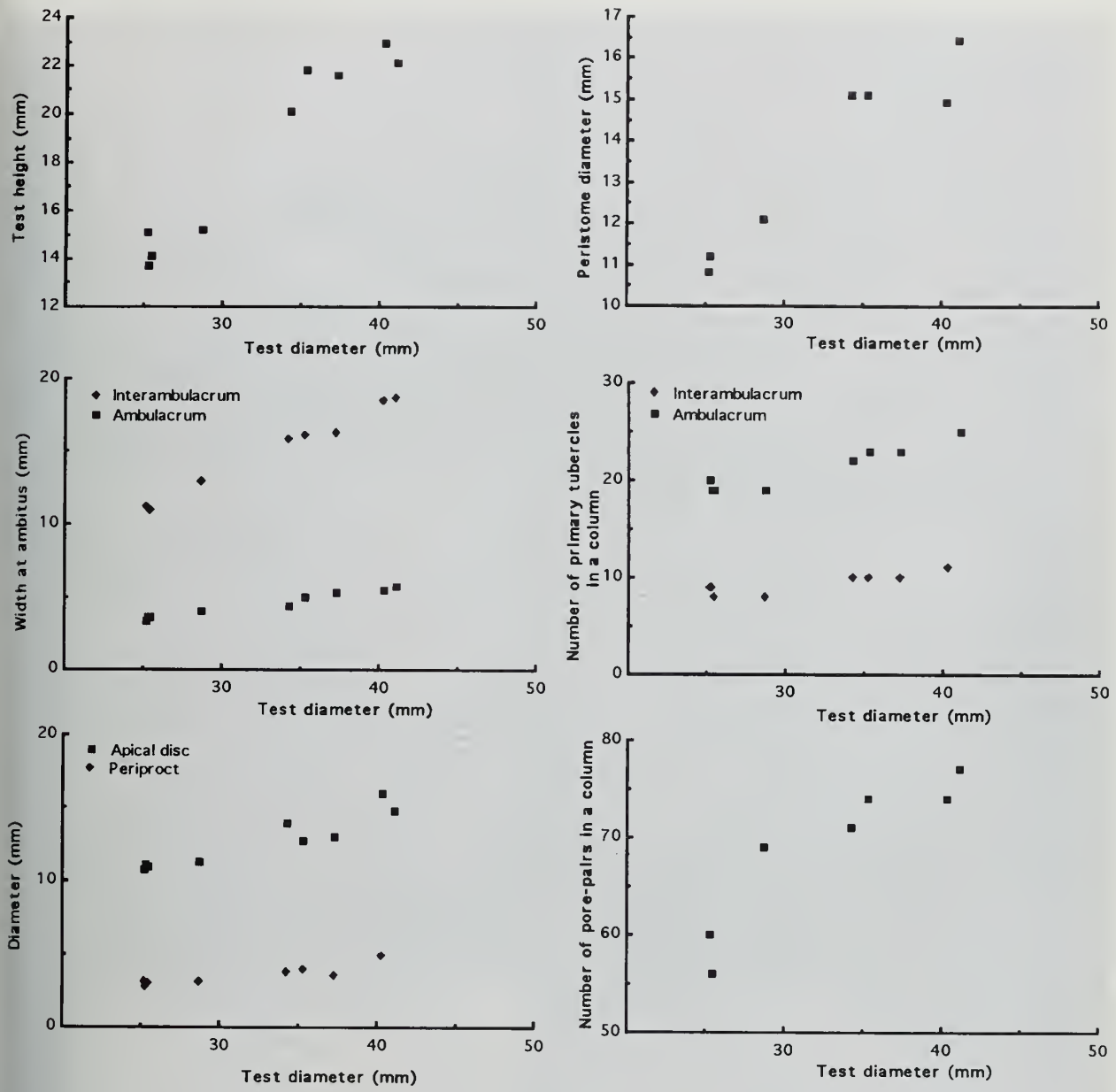


Fig. 17 Biometric data for *Goniopygus arabicus* sp. nov.

beyond the tip of the apical disc platform, though still within the genital plate (Figs 18A, B). Ocular plates are relatively large and are insert. All plates are flat and smooth, without ornamentation. The periproct is oval and lies slightly posterior of centre. It is approximately 9–12% of the test diameter in width along the anterior-posterior axis. In the great majority of specimens the opening is trigonal and there are three perianal tubercles on genital plates (Pl. 7, fig. 1). However, there is a single specimen (BMNH EE3983) that has five perianal tubercles (Pl. 6, fig. 9) and one that has four, thus the number of tubercles is not invariant.

The ambulacra are 13–14% of the test diameter in width at the ambitus. All plates are compound and trigeminate, with a demiplate and two full elements (Fig. 18D). The two major elements carry a single primary tubercle and the upper also has a perradial secondary tubercle in addition (Fig. 18E). The perradial tuberculate zone thus is composed of an outer series of primary tubercles alternating with a distinct inner series of secondary tubercles (Pl. 7, fig. 3). All tubercles are imperforate and non-crenulate. Below the ambitus pore-pairs are small and oval and become crowded close to the peristome to form a relatively well-developed phyllode (Pl. 7, fig. 5). At the ambitus pore-pairs become markedly more elongate and the individual pores more widely separated. Individual pores in a pore-pair are distinctly conjugate in larger individuals. There are no sphaeridial pits. There are 56 pore-pairs and 19 primary tubercles in a column at 25 mm test diameter, rising to 77 pore-pairs and 25 primary tubercles at 41 mm test diameter (Fig. 17).

Interambulacra are broad and each plate carries a large

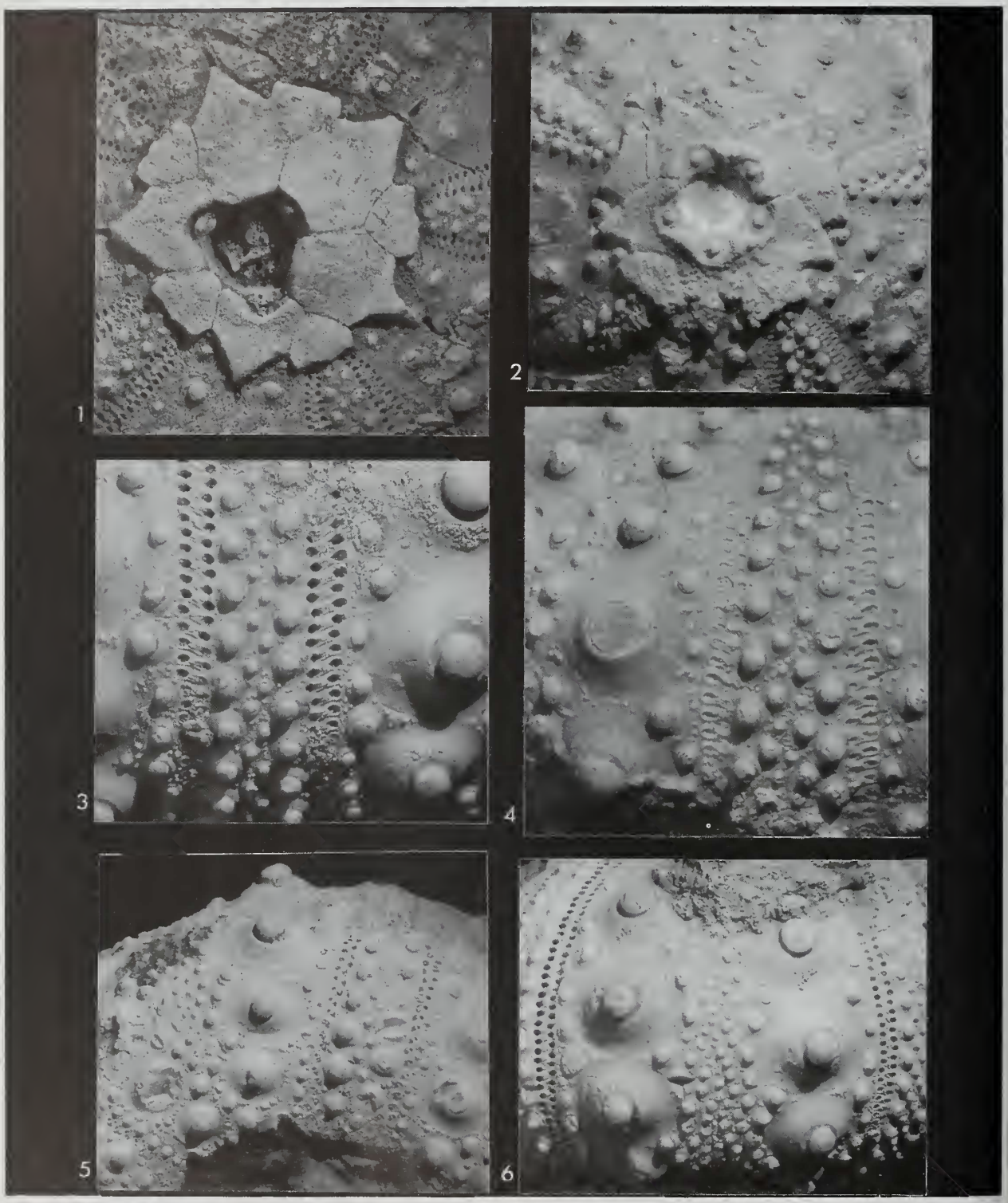


PLATE 7

Figs 1, 3, 5, 6 *Goniopygus arabicus* sp. nov. **1, 2,** BMNH EE4012, holotype; apical disc, × 5. Jebel Rawdah, section 3, bed 2. **3, 6,** BMNH EE4015, paratype; **3**, detail of ambulacrum at ambitus, × 5; **6**, detail of interambulacrum at ambitus, × 3. Jebel Thanais, lowest 1 m of the Simsima Formation. **5**, BMNH EE3997, adoral detail, × 3·5. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation.

Figs 2, 4 *Goniopygus superbus* Cotteau & Gauthier. L12680, Lambert Collection, Geology Department, Université de Paris VI, Paris; **2**, apical disc, × 4; **4**, detail of ambulacrum at ambitus, × 6. Derré-i-Chahr, Iran.

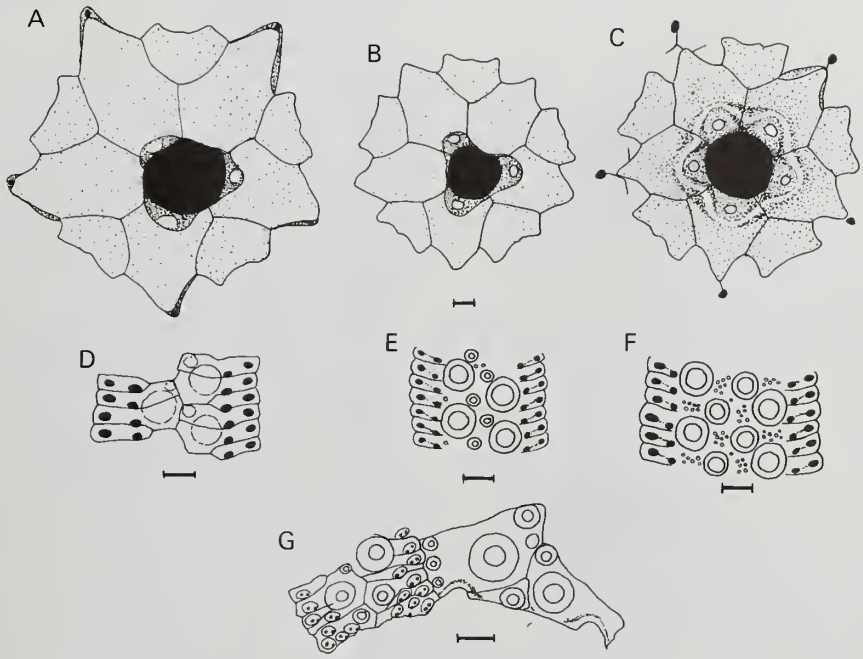


Fig. 18 Camera lucida drawings of *Goniopygus* species. **A, B** apical disc plating of *Goniopygus arabicus* sp. nov.; A, BMNH EE4017; B, BMNH EE4005. **C, F,** apical disc plating and ambital ambulacral tuberculation of *Goniopygus superbus* Cotteau & Gauthier, LI2680, Geology Department, Universite de Paris VI; Senonian, Derre-i-Chahr, Iran. **D, E,** ambital ambulacral plating, *Goniopygus arabicus* sp. nov.; D, BMNH EE4017; E, BMNH EE4005. **G**, *G. arabicus* sp. nov., adoral plating, ambulacrum to left, BMNH EE3986. Scale bars = 1 mm.

primary tubercle. At the ambitus interambulacral width is 42–46% of the test diameter. There are 8 plates in a column at 25 mm diameter, rising to 11 at about 40 mm test diameter (Fig. 17). Primary tubercles are stout, imperforate and non-crenulate at the ambitus, but reduce sharply in size adapically so that the top three or four tubercles are very small. At the ambitus they are surrounded by about 6 widely-spaced scrobicular tubercles (Pl. 7, fig. 6). Down the interradius there is a single column of secondary tubercles on each plate. Adorally both columns of plates reach the peristomial margin and there is no primordial plate (Fig. 18G).

The peristome is slightly invaginated and is 37–44% of the test diameter in diameter (mean = 42%, SD = 2·6%, N = 7). Buccal notches are relatively small and poorly differentiated, with only a weak rim.

Remarks. This species was described under the name *Goniopygus superbus* Cotteau & Gauthier by Kier (1972) and Ali (1989). It differs from that species in several important respects. Firstly, the apical disc of *G. superbus* has a larger periproctal opening and has either five, or rarely four perianal tubercles (Pl. 6, figs 1, 2; Pl. 7, fig. 2; Fig. 18C). These perianal tubercles face upwards and the adjacent portions of the genital plates are raised in the form of a very characteristic stellate rim. The radial portions of this rim project upwards as blunt denticles. Furthermore, the apical disc plates of *G. superbus* are covered in fine granular ornament. The gonopores in all specimens studied open not in the genital plates, but within the interambulacral plates some one or two plates distant from the apical disc (Fig. 18C). Finally, the ambulacral tuberculation affords an easily distinguishable character: in *G. superbus* the ambulacra are wide and the inner series of secondary tubercles almost as large as the primary tubercles, whereas in *G. arabicus* the ambulacra are narrow and the secondary tubercles very much smaller (compare Pl. 7, fig. 3 and Fig. 18E, with Pl. 7, fig. 4 and Fig. 18F). Finally, in *G. superbus* there are zones of small miliary granules separating successive tubercles which are totally absent in *G. arabicus*.

Genus *MIMIOSALENIA* gen. nov.

Type species. *Mimiosalenia quinquetuberculata* sp. nov.

Diagnosis. A goniopygid with a perianal tubercle on each genital plate and pits along apical disc sutures. Ambulacra bigeminate except adorally where occasional simple plates are intercalated.

Occurrence. Known only from the late Cretaceous (Maastrichtian) of Jebel Faiyah, section 1, western Oman Mountains.

Remarks. This genus is closely related to *Goniopygus* on account of its distinctive apical disc plating. The five gonopores lie immediately beyond the genital plates and open in the interambulacra. The genital plates of the apical disc have perianal tubercles identical to those of *Goniopygus* and the stellate ridge surrounding them is very reminiscent of that seen in *G. superbus* Cotteau & Gauthier. However, there are well-developed sutural pits both at triple junctions and mid-length along the plate sutures on all apical disc plates, which

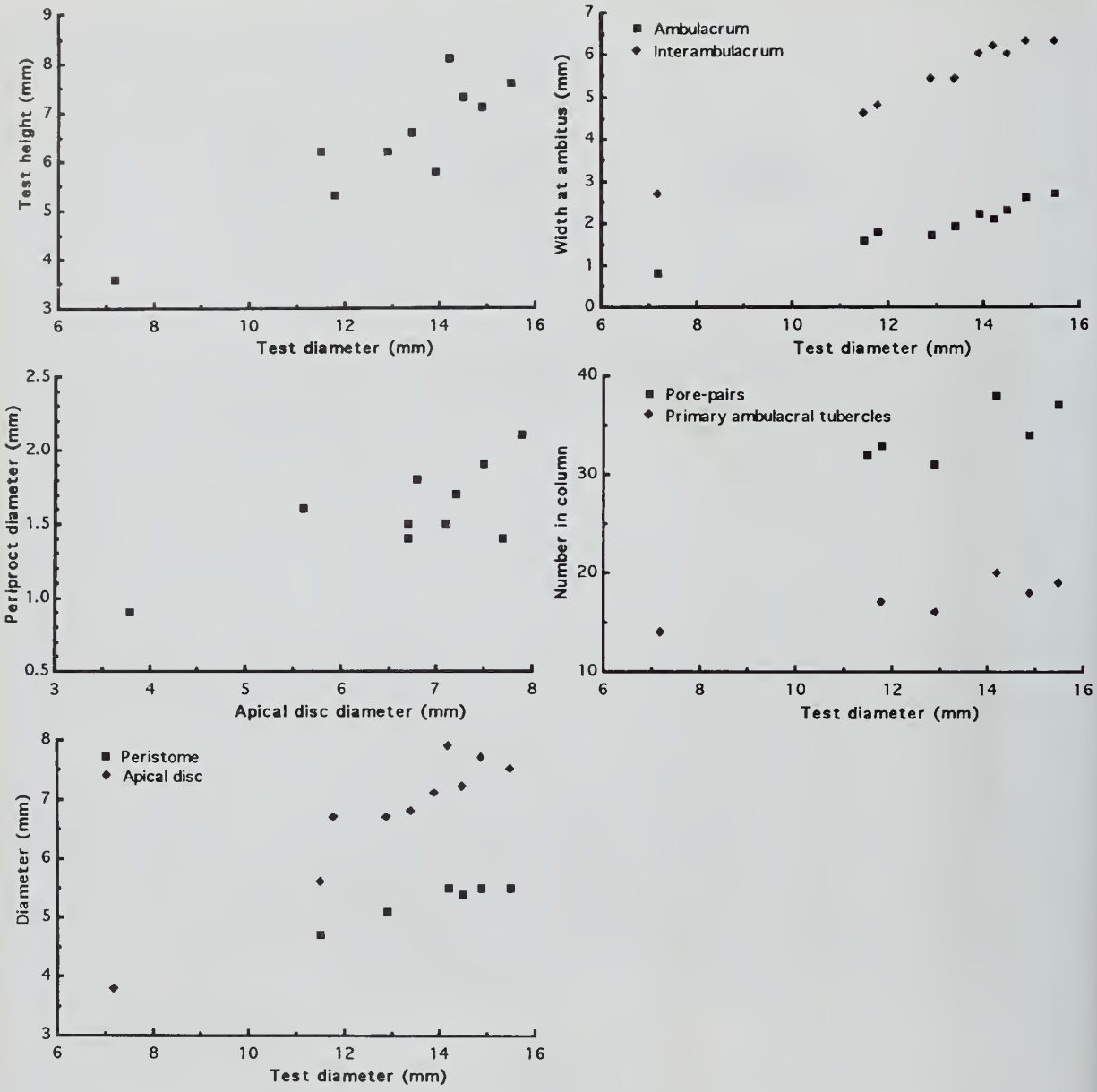


Fig. 19 Biometric data for *Mimiosalenia quinquetuberculata* sp. nov.

are often seen in saleniids but are never seen in *Goniopygus*. Another major difference between *Goniopygus* and *Mimiosalenia* is that the ambulacra of *Goniopygus* are trigeminate or occasionally quadrigeminate, whereas those of *Mimiosalenia* are strictly bigeminate, except close to the peristome where plating tends to become unigeminate. Again, bigeminate plating is typical of saleniids. All ambulacral plates in *Mimiosalenia* reach the perradius and are approximately equal in size, whereas in *Goniopygus* there is a demiplate and the other two plates in each triad are unequal in size.

Despite the similarities to *Salenia*, *Mimiosalenia* lacks a suranal plate and has the highly characteristic apical disc structure of a goniopygid. For this reason I believe it to be a derived goniopygid that has developed sutural pitting and bigeminate plating through the loss of the demiplate in each triad.

Mimiosalenia quiquetuberculata sp. nov Pl. 5, figs 4–10, 12; Figs 19, 20

TYPES. Holotype, BMNH EE3981; paratypes, BMNH EE3971, EE3974, EE3977–78, EE3980, EE3982, EE5014–17.

MATERIAL STUDIED. Biometric data is taken from the type series. In addition there are six other specimens.

OCCURRENCE. The species is known only from bed 7, section 1b, Jebel Faiyah, western Oman Mountains.

DIAGNOSIS. As for generic diagnosis: apical disc with five perianal tubercles. Gonopores lie just outside the genital plates in the interambulacral areas.

DESCRIPTION. Tests range from 7·2 to 15·5 mm in diameter and are circular in outline. Test height is 42–57% of test diameter with the flatter tests possibly representing slightly crushed specimens (Fig. 19). In profile the apical disc is very slightly conical and the sides uniformly rounded so that the ambitus lies at about mid-height.

The apical disc is relatively large and raised above the coronal plates (Pl. 5, fig. 7). It is 48–57% of the test diameter across (Fig. 19) with the periproct more or less centrally positioned. Ocular plates are relatively large and square-ended. The five genital plates border the periproct and are bluntly pointed distally (Figs 20A, B). All plates are smooth and unornamented. Each genital plate has a single perianal tubercle adjacent to the periproct. The genital plates are raised to form a stellate rim surrounding these perianal tubercles (Pl. 5, figs 4, 6; Figs 20A, B). All five genital plates are approximately the same size. Gonopores open beyond the genital plates and are found immediately adjacent in the interambulacral zones (Fig. 20B). They are only present in the larger specimens, *ca.* 14 mm diameter. The periproct is subcircular in outline and measures 9–15% of the test diameter in width (Fig. 19).

Ambulacra are relatively broad and slightly concave perradially. They are 11–17% of the test diameter in width at the ambitus. From the apex to below the ambitus plating is strictly bigeminate (Pl. 5, fig. 12; Fig. 20C), with each element reaching the perradius (Fig. 20D). Each pair of elements bears a large primary tubercle. Close to the peristome there are occasional simple elements interspersed, each with a large primary tubercle. There are 31–32 pore-pairs and 16–17 primary tubercles in a column at 11·5–13 mm test diameter, rising to 37 pore-pairs and 19 primary tubercles at 15·5 mm test diameter (Fig. 19). The perradial zone of tuberculation is very broad and contains a mixture of secondary tubercles and granules, two or three abreast (Pl. 5, fig. 12; Fig. 20C). Adorally the pore-pairs are slightly more widely separated and there is no phyllode development whatsoever. Ambulacra hardly taper either adorally or adapically. There are no sphaeridial pits.

Interambulacra are 38–44% of the test diameter in width at the ambitus. There are seven plates in a column at 6·2 mm test diameter, rising to eight or nine at 15 mm test diameter. Each plate carries a large primary tubercle which is non-crenulate and imperforate. The most adapical two are generally very much smaller than the remainder. The primary tubercles have six scrobicular tubercles, three on each side, that are more or less contiguous (Pl. 5, fig. 12). The interradial zone is broad and slightly concave. It is occupied by a series of miliary tubercles, two to each plate (four abreast). There is no primordial plate adorally and both columns reach the peristomial border.

The peristome is circular, slightly invaginated and occupies 36–40% of the test diameter. Buccal notches are small and indistinct (Pl. 5, fig. 9).

Spines, lantern and perignathic girdle all unknown.

REMARKS. The biserial nature of the ambulacra and the characteristic apical disc structure make this species easy to distinguish from any other described here.

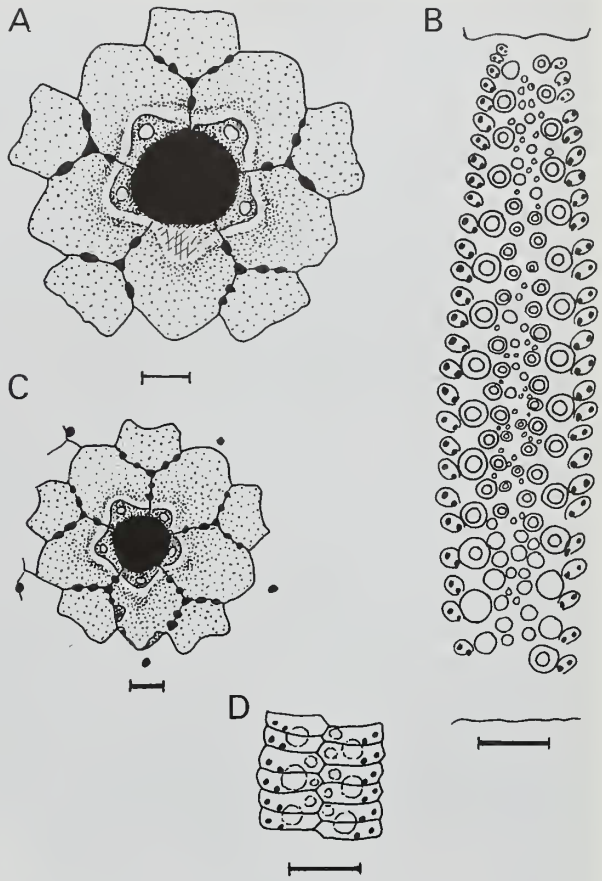


Fig. 20 Camera lucida drawings of plating in *Mimiosalenia quinquetuberculata* sp. nov. **A**, apical disc, BMNH EE3981; **B**, apical disc, BMNH EE3982; **C**, ambulacrum, from apical disc (top) to peristomial margin (bottom), BMNH EE3981; **D**, ambital ambulacral plating, BMNH EE5014–17. Scale bars = 1 mm.

Family **GLYPHOPNEUSTIDAE** Smith & Wright, 1993
Genus ***GLYPHOPNEUSTES*** Pomel, 1883

Glyphopneustes hattaensis Ali, 1992 Pl. 5, fig. 11; Pl. 8, figs 1–12; Figs 21, 22

1992a *Glyphopneustes hattaensis* Ali: 68, fig. 3.

TYPES. Holotype, the figured specimen, housed in the Geological Museum, University of Al Ain, United Arab Emirates.

MATERIAL STUDIED. 82 specimens, of which biometric data was taken from the following 30: BMNH EE3909, EE3913, EE3915, EE3919–20, EE3923–24, EE3926, EE3930–31, EE3934, EE3936–38, EE3940, EE3942–43, EE3945–47, EE3949, EE3953–54, EE3958, EE3960, EE3967–70.

OCCURRENCE. The type material all comes from Jebel Rawdah. This species was collected at the following levels:
Jebel Huwayyah, section 2: bed 1 (1).
Jebel Faiyah, section 1: bed 2 (1); bed 5 at base (1); bed 8 (9); loose approximately 10 m above base of the Simsima Formation (1).

Jebel Buhays section 1; loose, derived from lowest few metres of the Simsima Formation (50).
Jebel Thanais; lowest 2 m of the Simsima Formation (6).
Jebel Rawdah, section 1; bed 4 (1).
Jebel Rawdah, section 2; beds 9/10 (2); bed 11 (5); bed 13 (1); loose (6).
Jebel Rawdah, section 3; bed 2 (2); bed 5 (1).
Jebel Rawdah, section 4; bed 4 (1).

DESCRIPTION. Tests range in diameter from 10 to 30 mm, with the great majority around 18–24 mm diameter (Fig. 21). The test is circular in outline and depressed in profile, with a rounded ambitus, although some specimens are slightly more conical. Test height is 39–57% of the diameter (mean = 50%, SD = 4·0%, N = 30; Fig. 21). The ambitus lies at about mid-height.

The apical disc is highly sculpted and occupies 25–42% of the disc diameter (mean = 32%, SD = 1·2%, N = 30). It is proportionally larger in small individuals (Fig. 21). The periproct is large and central, occupying 30–50% of the apical disc diameter (mean = 40%, SD = 4·9%, N = 28). It is oval in outline with smoothly rounded edges (Pl. 8, figs 1, 2). The apical disc is dicyclic and all five genital plates are approximately equal-sized (Fig. 22B). There is a rim surrounding the periproct which bears a large central tubercle and two lateral tubercles. The gonopores open at the outer edge of the genital plates. The madreporite has a horse-shoe-shaped zone of madrepores that open around its margin (Fig. 22B).

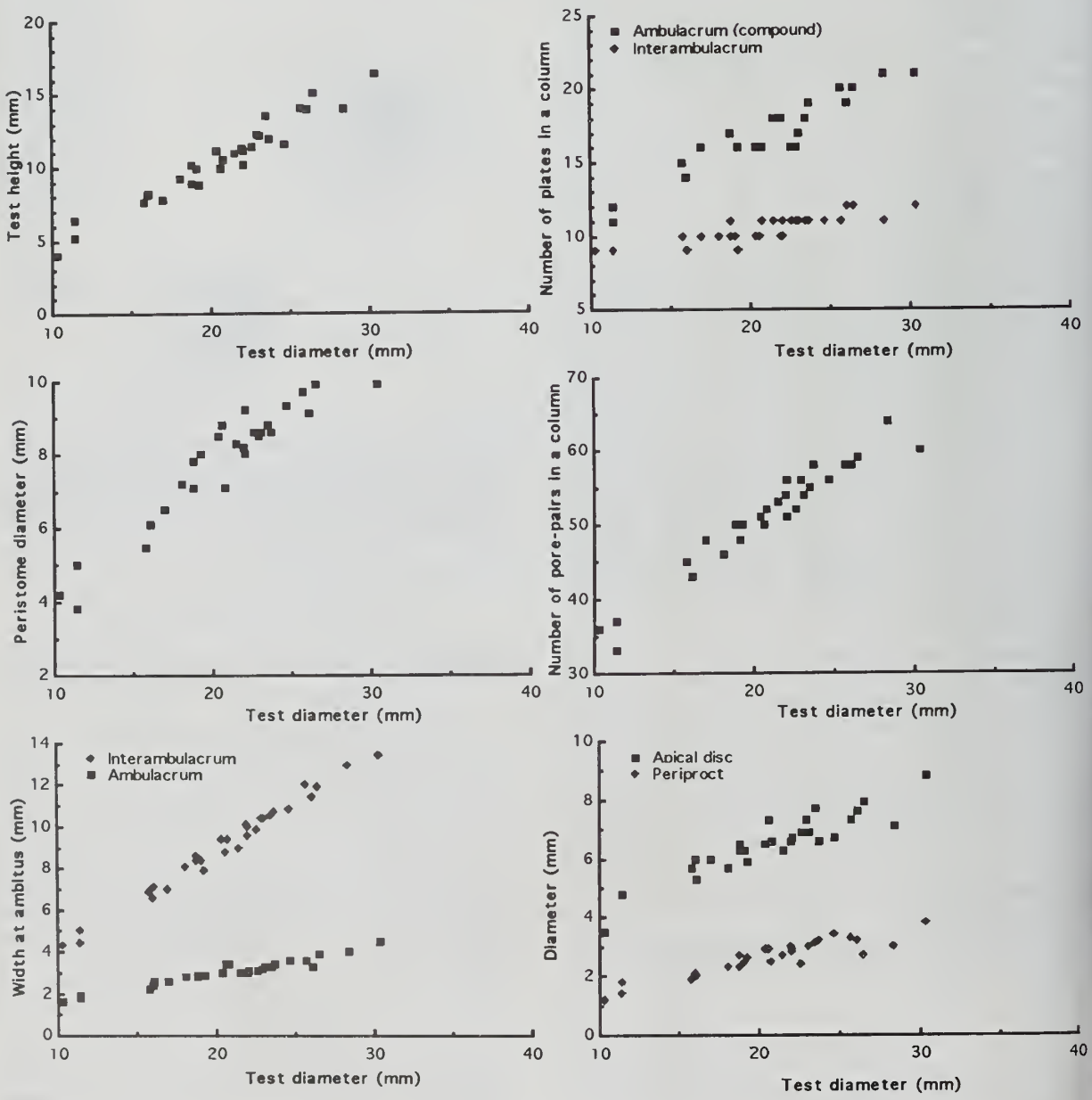
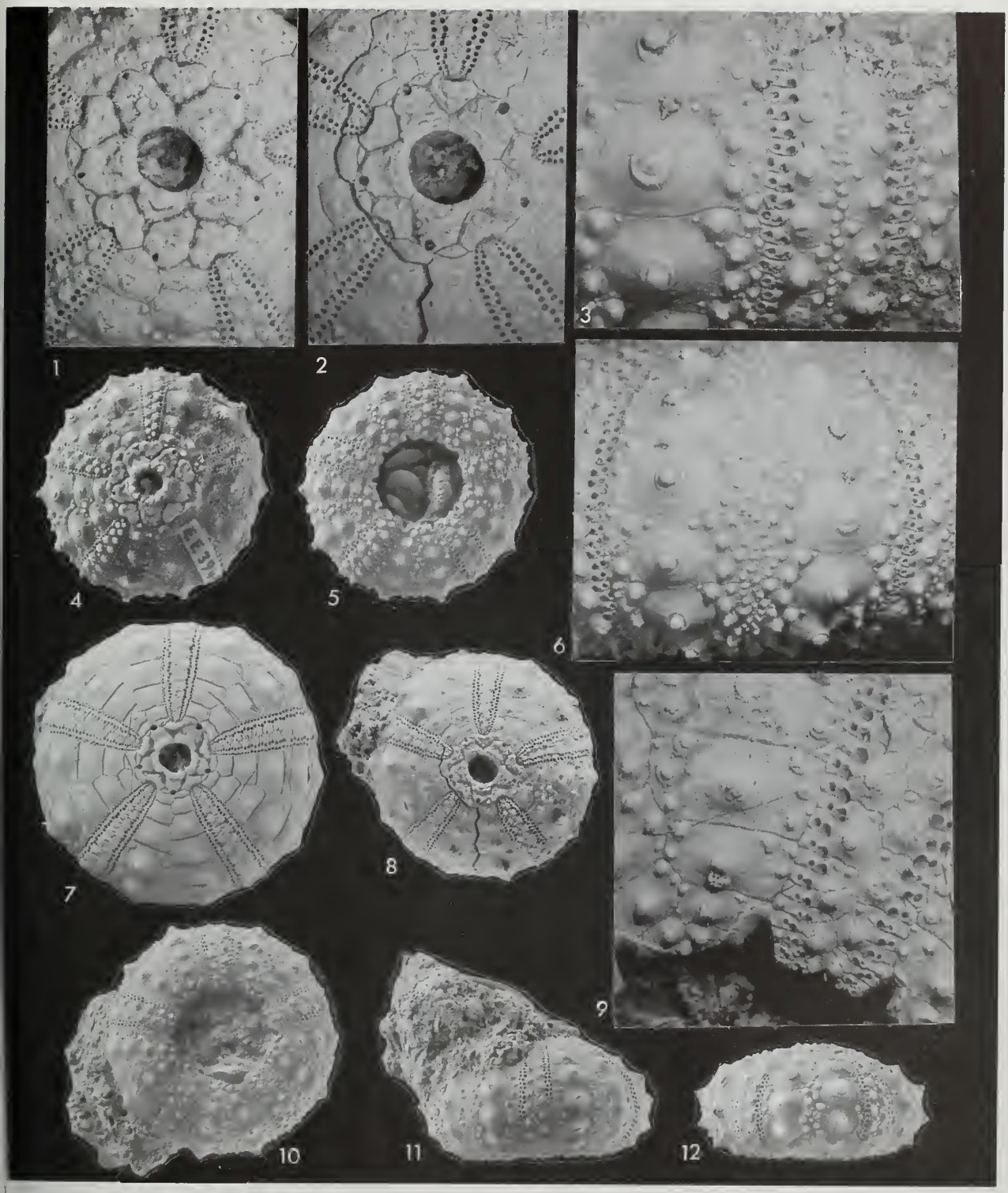


Fig. 21 Biometric data for *Glyphopneustes hattaensis* Ali.



LATE 8

igs **1–12** Glyphopneustes hattaensis Ali. **1**, BMNH EE3930; apical disc, × 6. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation. **2, 8,** BMNH EE3943; **2**, apical disc, × 5; **8**, apical, × 2. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation. **3, 6, 9,** BMNH EE3915; **3**, ambital detail of ambulacrum, × 6. **6**, ambital detail of interambulacrum, × 4; **9**, peristomial detail, × 6. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation. **7,** BMNH EE3958; apical, × 2. Jebel Faiyah, section 1, 2 m above the base of the Simsima Formation. **10, 11**, BMNH EE4027; **10**, oral, × 2; **11**, lateral, × 2. Jebel Thanais, lowest 2 m of the Simsima Formation. **4, 5, 12,** BMNH EE3945; **4**, apical; **5**, oral; **12**, lateral; all × 3. Jebel Buhays, section 1, loose in the scree.

Ocular plates are heart-shaped. The sutures are all deeply incised and there are typically three small tubercles along the ocular/genital plate boundary within these depressed regions.

Ambulacra are 13–17% of the test diameter in width at the ambitus (Fig. 21). All plates are trigeminate and there is a single demiplate in each triad (Figs 22A, C). The two full elements bear a single large primary tubercle that is imperforate and non-crenulate. The upper element is smaller than the lower. Towards the peristome the demiplate has a shallow pit immediately perradial to the pore-pair, which marks the site of a sphaeridium (Pl. 8, fig. 3; Fig. 22D). There are four or five of these in each column. Pore-pairs are uniserially arranged and not noticeably enlarged ambitally and adapically. There is no pore crowding whatsoever close to the peristome. There are around 33 pore pairs and 11 primary tubercles in a column at 11 mm test diameter, rising to about 60 pore-pairs and 21 primary tubercles (Fig. 21). There is a single row of scattered miliary tubercles down the perradius.

Interambulacra are 39–46% of the test diameter in width at the ambitus (mean = 44%, SD = 1·8%, N = 30). There are 9 plates in a column at 10 mm test diameter, rising to 12 at 30 mm test diameter (Fig. 21). Ambital plates are much wider than tall and each bears a single large primary tubercle that is non-crenulate and imperforate (Pl. 8, fig. 6). The most adapical two or three plates have significantly smaller tubercles than the rest. The primary tubercles have three scrobicular tubercles on either side, but have confluent areoles within each column. Down the interradius there are two or three irregular rows of scattered secondary and miliary tubercles, forming a relatively broad granular zone (Pl. 8, fig. 6). Adorally both columns of plates reach the peristome and there is no primordial plate.

The peristome is rather small and not at all invaginated. It is 33–43% of the test diameter across (mean = 38%, SD = 2·9%, N = 27), proportionally smaller in larger individuals (Fig. 21). Buccal notches are relatively shallow.

REMARKS. Ali (1992a) gave a detailed description of this species but based on only six specimens. The large number of well-preserved specimens now to hand allows a detailed biometric description of this species for the first time. Ali specifically stated that sphaeridial pits were lacking in this species, yet in well-preserved specimens such pits can be seen. The difference between this species and the Cenomanian *G. problematicus* rest almost entirely on the apical disc ornamentation and the absence of sutural pits on the interambulacral plates of *G. hattaensis*. Although Fell & Pawson (1966) placed *Glyphopneustes* in the family Hyposaleniidae, and were followed by Smith & Wright (1990), it is now evident from the material available that *Glyphopneustes* is an arbacioid, and has been placed in its own family Glyphopneustidae by Smith & Wright (1993). It has the characteristic perianal tubercles and apical disc structure of that family, and also has a similar style of ambulacral plate compounding. The sphaeridial pits are shallow and clearly convergent with those in *Hyposalenia*.

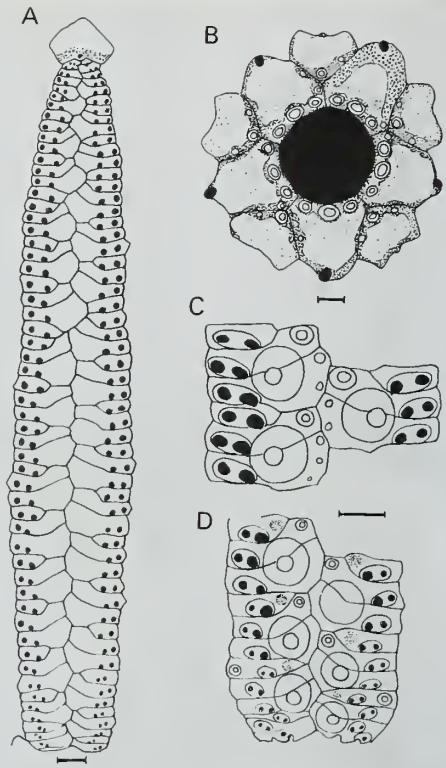


Fig. 22 Camera lucida drawings of plating in *Glyphopneustes hattaensis* Ali. **A**, Ambulacral plating, from ocular plate (top) to peristome margin (bottom), BMNH EE3926; **B**, apical disc, BMNH EE3912; **C**, ambital ambulacral plating, BMNH EE3915; **D**, adoral ambulacral plating, peristomial border at bottom, BMNH EE3915. Scale bars = 1 mm.

Family **ARBACIIDAE** Gray, 1835
Genus ***CODIOPSIS*** Agassiz, 1840

Codiopsis lehmannae sp. nov Pl. 9, figs 1–2; Pl. 12, figs 1–3; Fig. 23

DERIVATION OF NAME. After Mrs C. Lehmann, the finder of the holotype.

TYPES. Holotype, BMNH EE5033; paratypes (both incomplete test fragments), BMNH EE3439, EE3440.

OCCURRENCE. One specimen comes from Bed 15, section 1, Jebel Buhays, a second comes from bed 10 (top), section 2, Jebel Rawdah. The third specimen was found loose in the basal scree at Jebel Rawdah, section 2, and is almost certainly derived from the lowest few metres of the Simsima Formation (beds 3–10).

DESCRIPTION. The holotype is 18·3 mm in diameter and 8·2 mm in height (45% of the diameter). The two other specimens are larger, but incomplete, and by estimation would have been around 35–40 mm in test diameter. The base is flat, the upper surface domal, and the ambitus is very sharp and at the base. The apical disc is preserved in BMNH EE3440 and EE5033. It is dicyclic and firmly fixed to the corona (Pl. 12, fig. 1; Fig. 23C). The periproct is oval and 1·7 mm in diameter in the 18·3 mm diameter individual (9·3%).

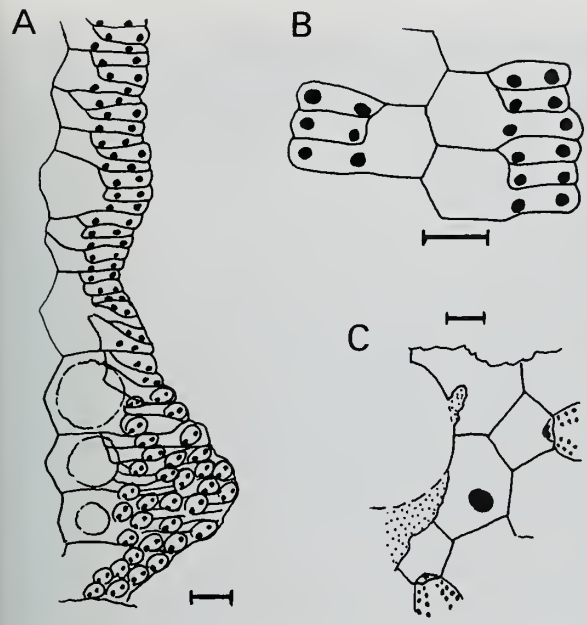


Fig. 23 Camera lucida drawings of plating in *Codiopsis lehmannae* sp. nov. **A**, ambulacral plating (one column only) from supra-ambital region (top) to peristomial margin (bottom), BMNH EE3439; **B**, aboral ambulacral plating, a little above the ambitus, BMNH EE3439; **C**, apical disc (incomplete) showing parts of two genital plates and two ocular plates, BMNH EE3440. Scale bars = 1 mm.

Ambulacra are narrow and parallel-sided above the ambitus, where they are trigeminate. Plate compounding is arbaciid in style with two demiplates (Fig. 23B). There is a single calcitic pustule on each triad (Pl. 9, figs 1, 2). Pores are small and widely-spaced, possibly conjugate (though preservation is too poor to be certain). Below the ambitus the pore-pairs reduce in width markedly (Fig. 23A) and the ambulacra widen into extensive phyllodes. The pore-pairs adorally are crowded and circular in outline with well-developed periporal muscle attachment areas. Compounding becomes polygeminate in a complex fashion (Fig. 23A) and there is a single large tubercle on each compound plate.

Interambulacral plates are geniculate at the ambitus and adoral portions bear a single primary tubercle. This arrangement creates a row of slightly downward-facing tubercles along the ambitus (Pl. 9, figs 1, 2). Adradial portions of these plates have fine secondary tuberculation. Adradial to the primary tubercles and continuing adapically along the adradial margin are very large calcite pustules. These reduce in size considerably above the ambitus and appear to continue adapically at least most of the way to the apical disc. The remainder of the adapical plates may have a pitted epistroma (traces are seen in BMNH EE3439), but the test is not well preserved.

Remarks. There is no doubt as to the generic placement of these specimens, on account of their distinctive pustules and arbaciid-style ambulacral compounding. Their sharp ambitus, flat base, extensive phyllodes and ambital ring of interambulacral tubercles are distinctive and are features unknown in other species. It differs from *Codiopsis brunei* Lambert, from the Maastrichtian of Maastricht, in being very much larger and in lacking well-developed aboral pustules. It comes closer to *C. disculus* Peron & Gauthier (and its synonyms *C. stephensoni* Cooke and *C. fontei* Vidal) from the late Campanian/Maastrichtian of Algeria, southern Spain, Senegal, Brazil and southern U.S.A., but differs from that species in having a more depressed profile, sharper ambitus and more distinct ambital ring of large tubercles. In *C. lehmannae* the primary interambulacral tubercles form a peripheral row, whereas in *C. disculus* the tubercles form a V-shaped arrangement extending adorally. Finally, in *C. lehmannae* the peristome appears highly scalloped.

Genus *HATTOPSIS* Ali, 1992

Hattopsis sphericus Ali, 1992 Pl. 9, figs 3–8; Pl. 10, figs 1, 2, 4; Fig. 24, 25B–D, 26B, 27A

1992b *Hattopsis sphericus* Ali: 694, fig. 3.

Types. Holotype 910401 in the Museum of the Geology Department, University of Al Ain, United Arab Emirates. Paratype 910402.

Material studied. 73 specimens, of which the biometric data was taken from the following: BMNH EE3658, EE3663, EE3690, EE3692–95, EE3698, EE3702, EE3705, EE3707–20.

Occurrence. The species was described from Jebel Rawdah (?section 1) by Ali (1992). Material collected *in situ* is as follows:

Jebel Faiyah, section 1: bed 7 (1); bed 8 (pycnodont level) (8).

Jebel Rawdah, section 1: bed 3 (22); bed 4, mostly towards top and base of bed 5 (44).

Jebel Rawda, section 2: bed 11 (2); loose in scree at base of section (1).

Diagnosis. A spherical arbacioid with a reticulate epistromal ornamentation. Every third ambulacral pore-pair reduced in size. Two interambulacral tubercles on each plate. Peristomial rim elevated as a lip interradially.

Description. Tests range from 12·0 to 20·8 mm in diameter (Fig. 24) and are circular to rounded pentagonal in outline. Test height is 60–83% of the diameter (mean = 74%, SD = 6·5%, N = 16), and tests are globular in profile with a small base and apex (Pl. 10, fig. 2).

The apical disc is dicyclic and occupies 23–33% of the test diameter (mean = 27%, SD = 2·4%, N = 14). The periproct is oval in outline and 9–12% of the test diameter in diameter. Ocular plates project slightly beyond the ring of genital plates (Pl. 10, fig. 2; Figs 25B, C). Genital plates are large and flat except around the periproctal margin where they are raised to form a rim. All genital plates are similar in size. The madreporite pores extend over most of genital plate 2. Well-preserved specimens show a reticulate pattern of ridges and pits (Pl. 10, fig. 2).

Ambulacra are 20–24% of the test diameter in width at the ambitus (Fig. 24). They are compound throughout with trigeminate plating. Close to the peristome both upper and lower elements are demiplates, but elsewhere it is only the upper element that is a demiplate (Fig. 26B). This demiplate has a pore-pair that is very much smaller than those on the other two elements. Each triad has a single large primary

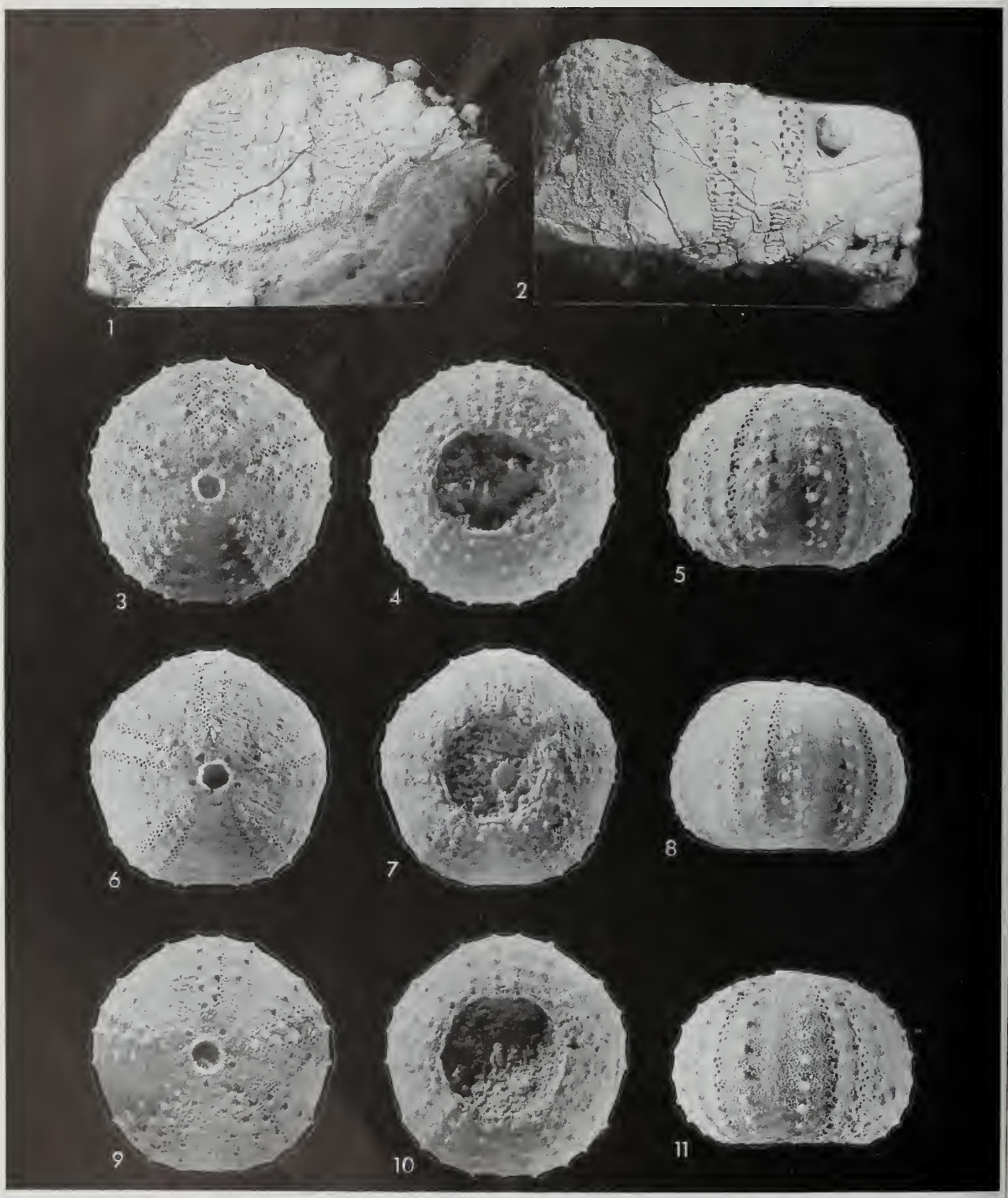


PLATE 9

Figs 1, 2 *Codiopsis lehmannae* sp. nov. BMNH EE3439, paratype; **1**, oral; **2**, lateral; both × 3. Jebel Buhays, section 1, bed 15.

Figs 3–8 *Hattopsis sphericus* Ali. **3–5**, BMNH EE3710; **3**, apical; **4**, oral; **5**, lateral; all × 3. Jebel Rawdah, section 2, bed 11. **6–8**, BMNH EE3712; **6**, apical; **7**, oral; **8**, lateral; all × 3. Jebel Rawdah, section 2, bed 11.

Figs 9–11 *Hattopsis paucituberculatus* sp. nov. BMNH EE3683, holotype; **9**, apical; **10**, oral; **11**, lateral; all × 3. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation.

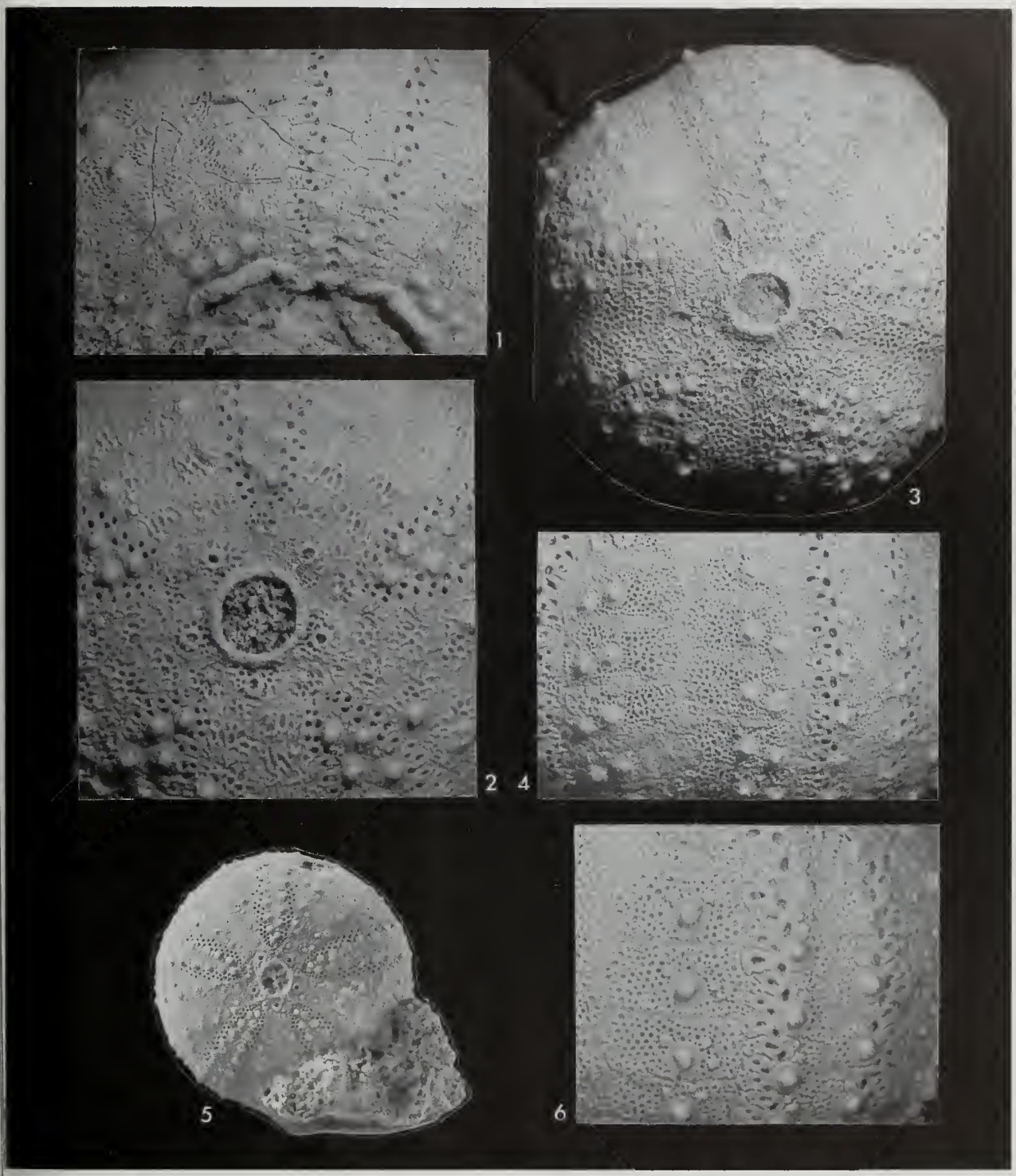


PLATE 10

Figs 1, 2, 4 *Hattopsis sphericus* Ali. BMNH EE3660; **1**, adoral detail showing sphaeridial pits at perradius and peristomial lip, × 6; **2**, apical disc, × 6; **4**, detail of ambital interambulacrum, × 6. Jebel Faiyah, section 1, bed 11.

Fig. 5 *Noetlingaster paucituberculatus* (Noetling). BMNH EE3680, juvenile, apical view, × 4 (see also Pl. 11, Figs 4, 5). Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation.

Figs 3, 6 *Hattopsis paucituberculatus* sp. nov. **3**, BMNH EE3672, paratype, adapical detail, × 7. Jebel Faiyah, section 1, bed 2. **6**, BMNH EE3682, paratype; ambital detail, interambulacrum to left, × 6. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation.

tubercle. There is a small secondary tubercle on the perradial margin of the lower element but other miliaries and secondary tubercles are absent. The perradius is ornamented with a reticulate pattern of ridges and shallow pits (Pl. 10, fig. 4). Close to the peristome there are up to four sphaeridial pits arranged uniserially down the perradius (Pl. 10, fig. 1). There are 33 pore-pairs and 10 primary tubercles in an ambulacral column at 12 mm test diameter, rising to 45–50 pore-pairs and 14–16 primary tubercles at 20–21 mm diameter (Fig. 24). No phyllodes nor any hint of pore-pair crushing is seen towards the peristome, and the pore-pairs themselves become much smaller adorally (Pl. 9, figs 4, 7; Fig. 26B).

Interambulacra are 36–40% of the test diameter in width at the ambitus. Plates are wider than tall and carry two small primary tubercles placed towards the adradial margin (Pl. 10, fig. 4; Fig. 27A). The tubercles in each pair are contiguous but are well separated from pairs of tubercles on other plates. There are no secondary or miliary tubercles, the remainder of the plate being covered in the same reticulate ornament of ridges and pits. At the peristome edge the interambulacra are thickened to form a distinct lip (Pl. 10, fig. 1). There is a single T-shaped primordial interambulacral plate forming the border to the peristome (Fig. 25D). There are 11 interambulacral plates in a column at 12 mm diameter, rising to 14 or 15 at 20–21 mm test diamater (Fig. 24).

The peristome is not at all invaginated and is 38–48% of the test diameter across (mean = 43%, SD = 3·1%, N = 13). Buccal notches are very slight and the raised interambulacral rim forms the most prominent feature (Pl. 10, fig. 1).

REMARKS. Ali (1992b) gave a detailed description of this species but new features reported here for the first time

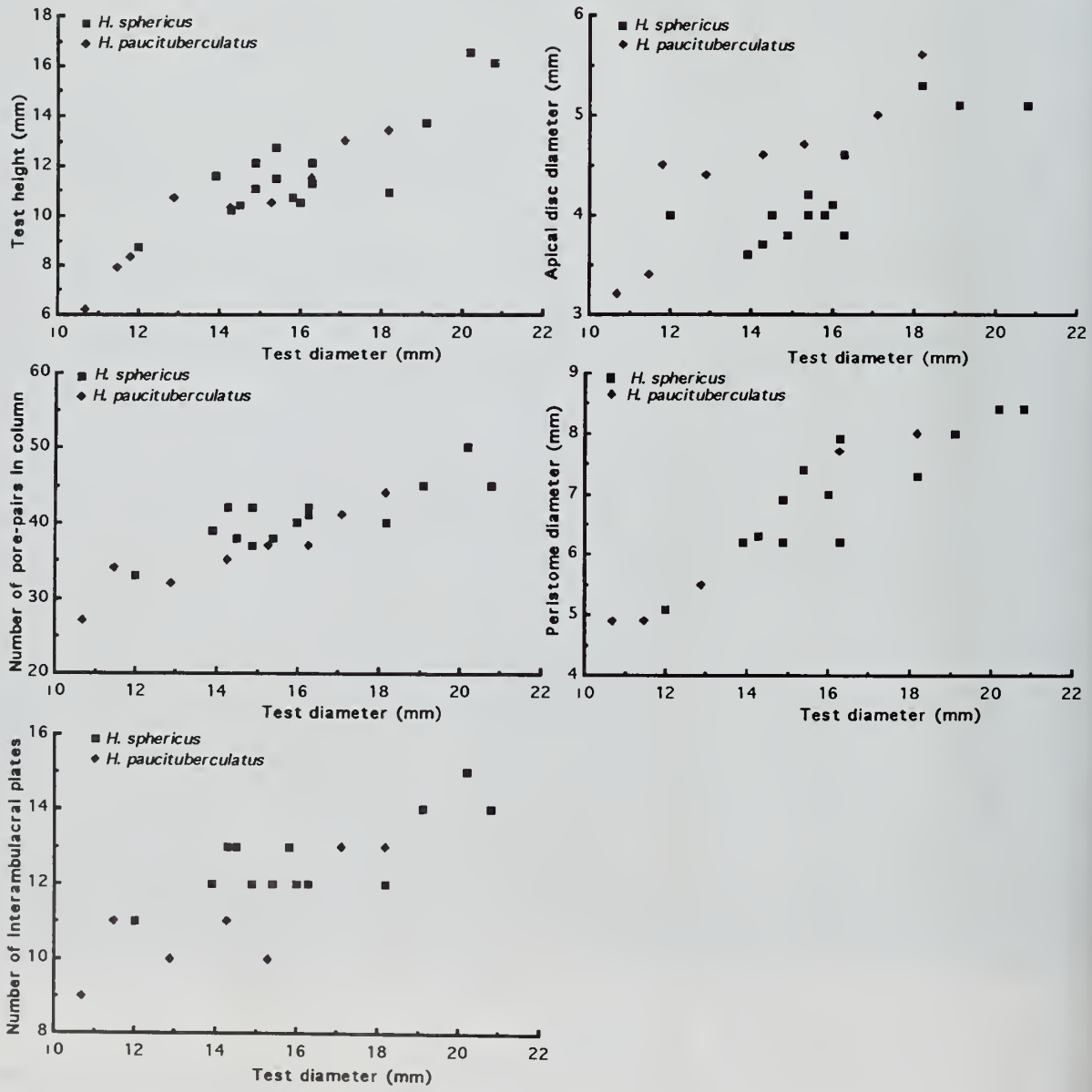


Fig. 24 Biometric data for *Hattopsis sphericus* Ali and *Hattopsis paucituberculatus* sp. nov.

include the perradial uniserial row of sphaeridial pits, the large T-shaped primordial interambulacral plate and the extensive development of reticulate ornamentation. The primordial plate, the uniserial and perradially positioned sphaeridial pits and the style of ambulacral compounding clearly place *Hattopsis* in the Arbaciidae. The reduction of one pore-pair in each triad and the presence of primary interambulacral tubercles above the ambitus separate *Hattopsis* from *Codiopsis*, which it resembles. *Hattopsis* comes most close in structure and appearance to juveniles of *Noetlingaster*, but differs from them in having fewer interambulacral tubercles at comparable sizes, and in being more globular in profile.

Hattopsis paucituberculatus sp. nov. Pl. 9, figs 9–11; Pl. 10, figs 3, 6; Pl. 11, fig. 9; Figs 24, 25A, 26A, 27B

TYPES. Holotype EE3683, paratypes, EE3682, EE3678, EE3688, EE3684–85.

MATERIAL STUDIED. There are 22 specimens in addition to the types. Biometric data is based on the following specimens: BMNH EE3672, EE3675, EE3678–79, EE3682–85, EE3688.

OCCURRENCE. This species was found at the following localities and horizons:
Jebel Faiyah, section 1: bed 2 (12).
Jebel Buhays section 1: in scree derived from lowest beds of the Simsima Formation (11); base of bed 12 (1).
Jebel Buhays, section 2: loose in scree, derived from lowest 3 m of the Simsima Formation (1).
Jebel Buhays, section 3: basal beds of the Simsima Formation (2).
Jebel Aqabah: bed 1 (1).
Jebel Rawdah, section 2, bed 8 (1); loose in scree derived from lowest part of section (1).

DIAGNOSIS. A species of *Hattopsis* with only a single interambulacral tubercle on each interambulacral plate at all sizes.

DESCRIPTION. Tests are 6·2 to 18·2 mm in diameter and circular to rounded pentagonal in outline (Pl. 9, figs 9–11). Test height is 58–83% of test diameter (mean = 71%, SD = 6·7%, N = 9) and in profile the test appears globular.

The apical disc is dicyclic, like that of *H. sphericus* (Fig. 25A). It is 28–37% (mean = 31%) of test diameter in diameter and there is an elevated rim around the periproct margin (Pl. 10, fig. 3). Gonopores are generally rather larger and more oval than those of *H. sphericus*.

Ambulacra are 20–25% of the test diameter in width at the ambitus and the ambulacral compounding is as in *H. sphericus* (Fig. 26A). There are 27 pore-pairs and 8 tubercles in a column at 10·7 mm test diameter, rising to 44 pore-pairs and 14 tubercles at 18·2 mm test diameter (Fig. 24). Aborally from the ambitus, the pore-pair on the upper demiplate in each triad is greatly reduced in size (Pl. 10, fig. 6; Fig. 26A). Adorally all pore-pairs become small and they remain uniserial to the peristome edge.

Interambulacra are 36–39% of the test diameter in width. Each plate carries a small primary tubercle, situated towards the adradial margin. (Pl. 10, fig. 6; Fig. 27B). The remainder of the plate is covered in fine reticulate ridges and pits. There are no secondary tubercles developed, even in the largest specimens.

The peristome is 43–47% of the test diameter in diameter and has the usual interambulacral lip and shallow buccal notches.

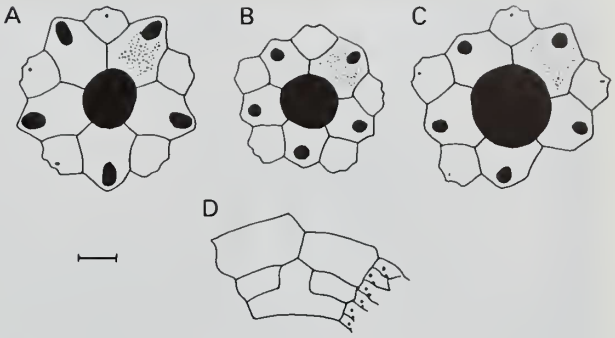


Fig. 25 Camera lucida drawings of plating in *Hattopsis*. **A-C**, apical discs; A, *H. paucituberculatus* sp. nov, BMNH EE3672; B, *H. sphericus* Ali, BMNH EE3692; C, *H. sphericus* Ali, BMNH EE3681. **D**, *H. sphericus*, BMNH EE3693, adoral interambulacral plating, peristomial edge at base. Scale bar = 1 mm.

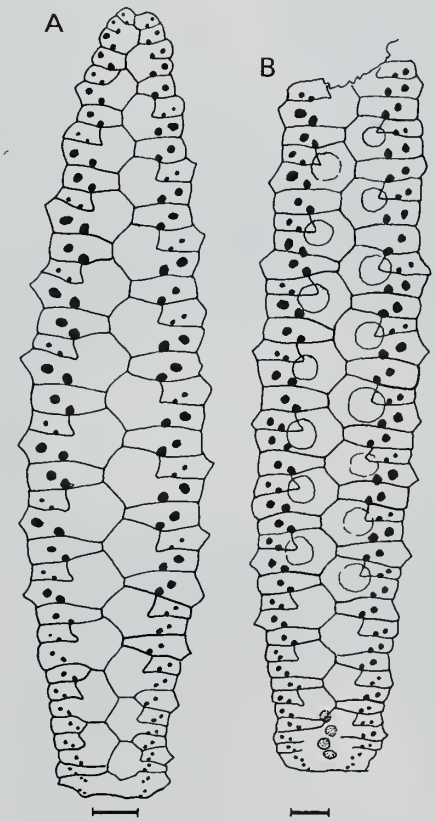


Fig. 26 Camera lucida drawings of ambulacral plating in *Hattopsis*. **A**, *H. paucituberculatus* sp. nov., complete ambulacrum from apical disc (top) to peristomial margin (bottom); BMNH EE3678; **B**, *H. sphericus* Ali, ambulacrum from close to apical disc (top) to peristomial margin (bottom); BMNH EE3659. Scale bars = 1 mm.

REMARKS. This species resembles *H. sphericus* in all details except that it has only a single interambulacral tubercle on each plate, rather than the two found on all specimens of *H. sphericus* greater than 12 mm. Although I have included

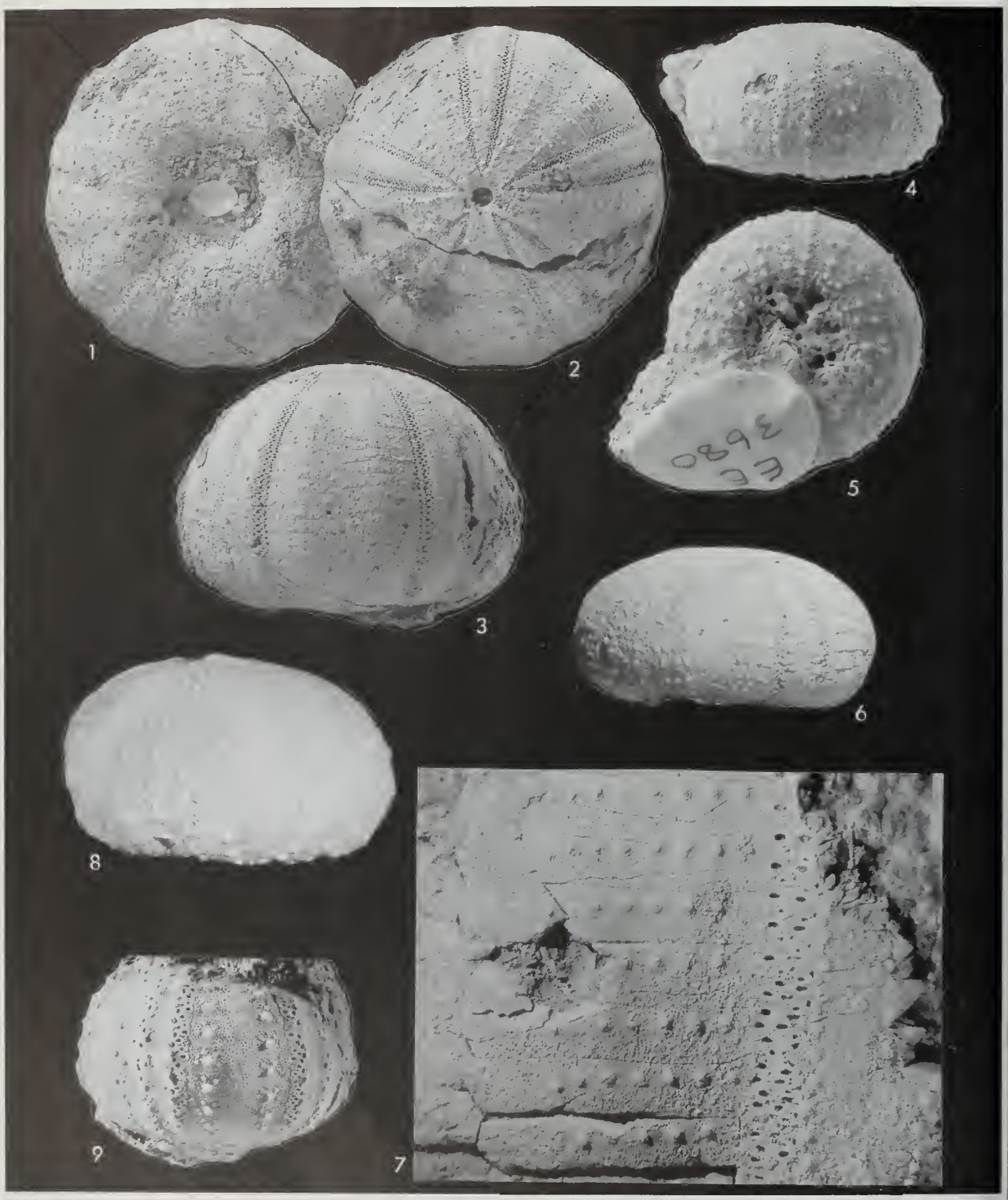


PLATE 11

Figs 1–3 *Noetlingaster emiratescus* Ali. BMNH EE3285; **1**, oral; **2**, apical; **3**, lateral; all × 1. Jebel Rawdah, section 4, bed 12.

Figs 4–7 *Noetlingaster paucituberculatus* (Noetling). **4**, **5**, BMNH EE3680 (juvenile); **4**, lateral; **5**, oral; both × 4. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation. **6**, BMNH EE3286 (juvenile), lateral view, × 4. Jebel Rawdah, section 2, bed 11. **7**, BMNH EE3282, detail of ambital region, adoral towards top and interambulacrum to left, × 4.

Fig. 8 ?*Noetlingaster* sp. BMNH EE3689, lateral, × 5. Jebel Huwayyah, section 2, beds 2–7.

Fig. 9 *Hattopsis paucituberculatus* sp. nov. BMNH EE3682, lateral view, × 3. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation.

some specimens smaller than 12 mm in this species, they could possibly turn out to be juveniles of *H. sphericus*. However, the majority of specimens are larger than 12 mm and the distribution of the two species is also not the same. Whereas *H. sphericus* is found predominantly at Jebel Rawdah, section 1, beds 3–4 and also in beds higher up the succession (bed 11) in section 2, as well as at the pycnodont level (bed 8) at Jebel Faiyah, *H. paucituberculatus* consistently occurs further down in the succession (basal beds of Jebel Buhays and Jebel Faiyah, and bed 8 in Jebel Rawdah, section 2). The two species are thus stratigraphically discrete.

Genus *NOETLINGASTER* Vredenburg, 1911

TYPE SPECIES. *Protechinus paucituberculatus* Noetling, 1897 by original designation.

REMARKS. *Noetlingaster* has previously been classified in the Stomechinidae on account of its imperforate tuberculation and dicyclic apical disc (e.g. Fell & Pawson 1966). However, it has a single large primordial interambulacral plate at the adoral end of each interambulacrum and a tuberculation style very similar to that of *Hattopsis*. Primordial interambulacral plates this well-developed are known only in the Arbaciidae. Finally, juvenile forms of *Noetlingaster* are extremely similar in appearance to *Hattopsis*, differing only in having a more depressed test profile and more interambulacral tubercles at corresponding sizes. Given the marked similarity between *Hattopsis* and *Noetlingaster* in apical disc, tuberculation, interradial epistroma and pore-pair development, there seem strong grounds for placing *Noetlingaster* as an arbaciid.

There are nine named species of *Noetlingaster*, all from the late Cretaceous. The type species *N. paucituberculatus* (Noetling, 1897) comes from horizon 4 (?Maastrichtian) in the Des Valley, Mari Hills, West Pakistan. Other species are: *N. emiratescus* Ali (1989), described from Jebel Rawdah, western Oman mountains; *N. sanfilippoi* Checchia-Rispoli (1930), *N. millosevichi* Checchia-Rispoli (1930) and *N. lamberti* Checchia-Rispoli (1930), all from the Maastrichtian of Gebel Misid, Tripolitania, Lybia; *N. globulus* Devries (1967) and *N. hemisphericus* Devries (1967), both from the Maastrichtian of Kahta, Turkey; *N. monteili* Gauthier (1901) from the 'Senonian' south of Bilma, Algeria; and *N. boulei* Lambert (1906) from the Maastrichtian of Marohite, Madagascar. Devries (1967) reviewed previous species and discussed their diagnosis. He laid particular emphasis on the arrangement of interambulacral tubercles, recognizing two groups: those with a single row of interambulacral tubercles on each plate, and those with a double row. He pointed out that the actual number of tubercles in each row varied ontogenetically and also according to position on the test.

All these species are closely related because of their highly distinctive ambulacral plate compounding and pore-pair arrangement (see below). However, all have been erected on the basis of very few specimens, often simply the holotype. Thus the intraspecific variability has never been properly documented. In addition, the relatively thin test means that specimens are rarely well preserved. The large collection of specimens from Jebel Rawdah allows ontogenetic variability to be assessed in this species complex for the first time.

There are significant differences in size between the species that have been erected, and these may account for some of the morphological variation described. *N. boulei* is described from the smallest specimen, only 49 mm in diameter. *N. globulus*, *N. hemisphericus* and *N. emiratescus* are all based on specimens ranging from 65–83 mm. The remainder are described from large individuals between 95 and 120 mm in diameter (Fig. 28). As many of the characters previously used for species discrimination can be shown to vary with size in the Omani populations, it is important that similar-sized individuals are compared when differentiating species.

Shape differences were used by Devries (1967) to separate some species. He identified species as either 'subconical' or 'rounded convex'. However, there seems to be considerable variation in this feature within the sample described here, and thus the character has little worth. It is also difficult to use in practice since specimens are often crushed or distorted during preservation.

Ambulacral differences have also been used for diagnosing species. *N. boulei* for example has just one primary tubercle on ambulacral plates, and this is found on alternate plates only. However, as Lambert's (1906) photographs show, ambulacral tuberculation is not consistent. Adoral compound plates all have a single primary tubercle, whereas, adapically, tuberculation is more irregular with occasional plates lacking primary tubercles. Considering the small size of *N. boulei* one would not expect more than a single tubercle to be developed, by comparison with the Omani sample. Furthermore, tuberculation is very irregular in the Omani population, especially adapically from the ambitus where it is relatively common to find primary tubercles missing from ocassional plates. Such irregular ambulacral tuberculation characterises all species and from about 60 mm test diameter upwards all species have plates bearing two or three tubercles irregularly arranged. Note that although Gauthier (1901) describes *N. monteili* as having eight rows of ambulacral tubercles, his figures show only four irregular columns and the ambulacral

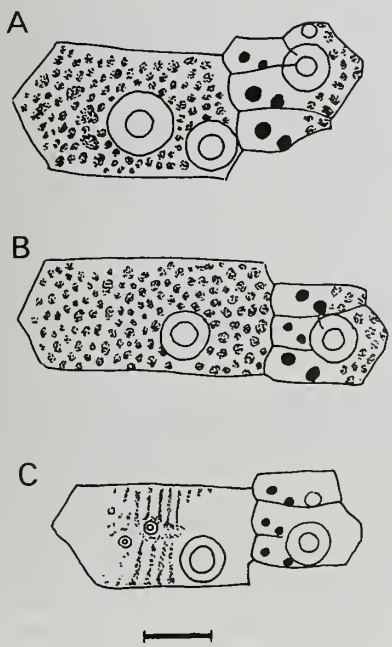


Fig. 27 Camera lucida drawings of ambital plating in *Hattopsis* and *Noetlingaster?* sp.: interambulacral plate on the left, ambulacral plate on the right. **A**, *Hattopsis sphericus* Ali, BMNH EE3693; **B**, *Hattopsis paucituberculatus* sp. nov., BMNH EE3683; **C**, *Noetlingaster?* sp., BMNH EE3689.

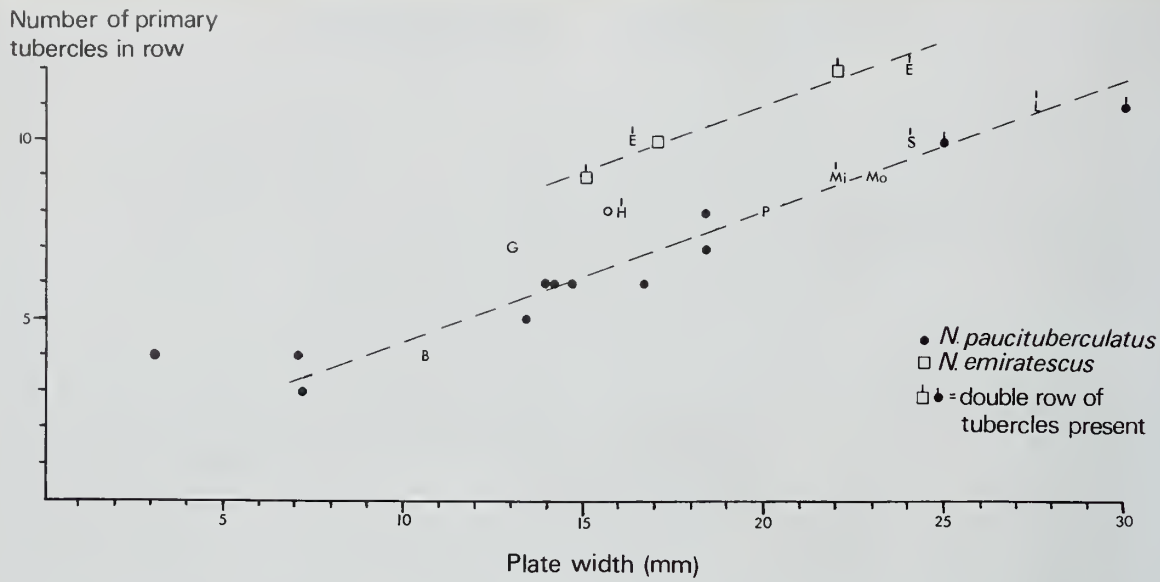


Fig. 28 Biometric data from *Noetlingaster* species. Type specimens for species are plotted as follows: B = *N. boulei* Lambert; E = *N. emiratescus* Ali (two syntypes); G = *N. globulus* Devries; H = *N. hemisphaericus* Devries; L = *N. lamberti* Checchia-Rispoli; Mi = *N. millosevichi* Checchia-Rispoli; Mo = *N. monteili* Gauthier.

structure does not differ from that seen in equivalent-sized Omani specimens.

Most emphasis has been placed on interambulacral tuberculation for differentiating between species. Devries (1967) recognized two species groups: those with just a single row of tubercles to each interambulacral plate and those with a double row. He also distinguished between those with a naked interradial zone of fine granulation and those with primary tubercles extending more or less to the interradius. Unfortunately, the Omani specimens also show considerable variation in these features. The majority simply have a single row of primary tubercles extending more or less to the perradius. From the ambitus adapically there may or may not be a naked zone free of primary tubercles and when present this zone may or may not extend below the ambitus. In many specimens it is difficult to observe tuberculation interradially because of weathering, and the same is probably true for the specimens on which other species are based. Single rows of tubercles are characteristic of *N. paucituberculatus*, *N. monteili*, *N. boulei* and *N. globulus*, whereas *N. sanfilippoi*, *N. millosevichi*, *N. hemisphaericus* and *N. emiratescus* all have two or three additional tubercles forming a second row adradially, and *N. lamberti* has a full double row of tubercles developed on all plates. All tuberculation styles, except that seen in *N. lamberti*, are encountered in the Omani sample. As can be seen from Fig. 28, there is a strong correlation between the number of tubercles on a plate and the plate width (which is proportional to test diameter). Furthermore, it is primarily the larger specimens that have a second row of tubercles developed adradially. However, it is not completely size-dependent since the 69 mm diameter specimen EE3279 has a well developed secondary row of tubercles whereas others of that size do not.

In conclusion, the variation observed within the 20 reasonably well-preserved specimens from the western Oman mountains is almost as great as that observed between the nine described species, each based on one or a few specimens only. The presence or absence of an interradial naked zone and the extent of this zone when present, the number of interambulacral tubercles in a row in proportion to the plate width and the development of a second row of primary tubercles to a plate are all variable. Similar variation of tuberculation has been found in both Turkey (Devries 1967) and Libya (Checchia-Rispoli 1930), but was used to distinguish 'species'.

By contrast the analysis of variation amongst Omani specimens suggests that tuberculation pattern may not be so rigidly developed. It does, however, support some subdivision of the genus. When tuberculation style is plotted against test diameter, two distinct growth trajectories emerge for Omani specimens (Fig. 28). In some specimens there are numerous densely-spaced tubercles with secondary tubercle rows present, even at 60 mm test diameter. Other specimens have more widely-spaced primary tubercles and only develop a secondary row of adradial tubercles on ambital plates at a very large size. Although these may simply represent end members of a continuous spectrum, the small sample does not indicate any significant overlap. Those with many tubercles also always lack a granular interradial zone, whereas those with relatively fewer tubercles typically have a naked zone. However, the development of this naked zone is quite variable, with some specimens showing a broad zone extending almost to the peristome, and others with the zone restricted to a narrow wedge-shaped area adapically. Measurements taken from the types of all nine species are plotted for comparison. The type species *N. paucituberculatus* falls into the growth series of forms with fewer tubercles, as do the types of *N. millosevichi*, *N. boulei*, *N. monteili*, *N. sanfilippoi*, and *N. lamberti*. The more densely tuberculate form corresponds to *N. emiratescus* and may also include *N. globulus* and *N. hemisphaericus*, although both plot in an intermediate position. (This may be due to inaccuracies in the magnifications for the camera lucida drawings of interambulacral plates given approximately by Devries (1967, pl. 2)).

Plotting those with a secondary row of tubercles to interambulacral plates shows that the secondary row appears at about 15 mm plate width in *N. globulus*/*N. emiratescus*, whereas it only develops at around 22 mm plate width in the *N. paucituberculatus* group.

The one anomolous specimen is BMNH EE3282, which has numerous small interambulacral tubercles, but a wide interradial granular zone. It falls in between the two growth series in Fig. 28.

In conclusion, only two species of *Noetlingaster* are recognized here:

(1) Forms to *ca.* 125 mm diameter with granular interradial zone developed adapically or throughout and a single row of relatively widely spaced interambulacral tubercles. Adradially, a second shorter row of tubercles is developed in larger specimens. These forms occur at Jebel Rawdah, section 2 from bed 11 to 14 and correspond to the form first described as *N. paucituberculatus* (Noetling).

(2) Forms to *ca.* 125 mm with a second row of interambulacral tubercles present adradially from about 60 mm test diameter, and no naked zone. At comparable sizes there are more interambulacral tubercles in a row than in the first species. This form occurs at Jebel Rawdah section 1, but at higher levels in the section than *N. paucituberculatus*. It has been described from the Oman Mountains under the name *N. emiratescus* Ali.

Noetlingaster paucituberculatus (Noetling, 1897) Pl. 10, fig. 5; Pl. 11, figs 4–7; Figs 28, 29, 30A–D, F, H, 31

1897 *Protechinus paucituberculatus* Noetling, 1897: 16, pl. 2, fig. 3, pl. 3, fig.1.
1898 *Noetlingia paucituberculata* Noetling; Lambert: 126.
1901 *Noetlingia Monteili* Gauthier: 191, pl. 3, figs 1–3.
1906 *Noetlingia Boulei* Lambert: 11, pl. 2, fig. 7.
1911 *Noetlingaster paucituberculata* Noetling; Vredenburg: 46.
1930 *Noetlingaster Millosevichi* Checchia-Rispoli: 14, pl. 2, figs 1, 2, pl. 4, figs 3, 4.
1930 *Noetlingaster Sanfilippoi* Checchia-Rispoli: 6, pl. 1, fig. 1, pl. 3, fig. 2, pl. 4, fig. 2.
1930 *Noetlingaster Lamberti* Checchia-Rispoli: 20, pl. 1, fig. 2, pl. 3, fig. 1, pl. 4, fig. 1.

Types. The type is the 95 mm diameter specimen described by Noetling (1897) from the late Cretaceous of the Mari Hills, West Pakistan.

Material studied. 19 relatively complete tests and 2 test fragments, including juveniles. The following ten specimens were used in the biometric analysis: BMNH EE3267, 3269, 3271–75, 3280, 3282 and 3286.

Occurrence. In the western Oman mountain area *N. paucituberculatus* was found at the following levels:
Jebel Rawdah section 1, base of bed 4 (juvenile).
Jebel Rawdah, section 2: bed 11 (3, plus fragments); bed 14 (5, plus fragments); bed 19 (2); bed 25 (4); bed 26 (2).
Jebel Buhays, section 1: loose in scree derived from lowest beds of the Simsima Formation (3, including one complete 13 mm diameter juvenile).

Outside the eastern Arabian peninsula this species is recorded from western Pakistan, Algeria, Libya and Madagascar.

Description. Tests range in diameter from 15 to 126 mm. They are more or less circular in outline, but very slightly depressed both interradially and adradially. Test height is 54–79% of test diameter (mean = 66%, SD = 7·2%, N = 10) and juveniles tend to have more depressed tests than adults. In profile the test is subconical, with a broad base, narrow apex and low ambitus (Pl. 11, figs 4, 6). The ambitus lies at about one quarter of the test height above the base.

The apical disc is relatively small, occupying only 13–16% of the test diameter in medium to large individuals (mean = 14%, SD = 1·2%, N = 6). It is proportionally larger in small individuals, occupying 19% of the test diameter in the 15 mm diameter specimen (Fig. 29). Disc plating is dicyclic (Figs 30A, B). The madreporite is very much larger than other genital plates and is densely covered in small pores. Each genital plate has a large oval gonopore which may be surrounded by a slight rim. The ocular plates are small and pentagonal, each with a small ocular pore. The periproctal opening is large and oval.

Ambulacra are straight and taper adapically. At the ambitus their width is 16–20% of the test diameter. Ambulacral plates are trigeminate throughout with a highly distinctive style of compounding (Figs 30C, D, F, H). The lowest element is large and occupies the full width. There is a smaller demi-plate above, which always carries a large pore-pair adradially and an even smaller, fully occluded element above that (Figs 30D, F). This arrangement is found along the entire length of the ambulacrum in all medium to large individuals, except at the very apex, where the occluded plate may reach the adradial suture. In smaller individuals both of the smaller elements are demiplates (Fig. 30H), while in BMNH EE3286, a juvenile of only 15 mm test diameter (Fig. 30F), the upper element extends to the perradial suture. There are no phyllodes nor any pore crushing towards the peristome. Each element carries a pore-pair, but only on the large primary element are these well-developed throughout (Pl. 11, fig. 7). The pore-pairs on the small occluded upper element are always reduced to rudimentary structures and in places may simply be represented by a single pore. The middle element usually has well-developed pore-pairs, but in larger individuals around the ambitus these may also be very much reduced in size (Fig. 30F). Pore-pair differentiation is hardly developed in the 15 mm diameter juvenile. Each compound plate usually carries a single primary tubercle close to the pore-zone. However, tuberculation is irregular and occasionally two tubercles occur to a plate. In the largest individuals most ambulacral plates carry two adradial primary tubercles, slightly offset on alternate plates. The perradial band is devoid of large tubercles above the ambitus, but this zone is relatively narrow, typically only some 15% of the interambulacral width. There are approximately 112 pore-pairs in a column at a test diameter of 32 mm, rising to around 180 at 80 mm test diameter (Fig. 29).

Interambulacral width at the ambitus is 41–47% of the test diameter. Plates are wide and low, and are slightly taller than ambulacral plates. There are 36 interambulacral plates in a column at 82 mm test diameter. The primary tubercle at the centre of the plate is set on a slight keel which runs down the midline of each column and is particularly prominent adapically. There are multiple small tubercles on each plate, three in the smallest individual (Pl. 11, fig. 4), rising to 11 in the

PLATE 12

Figs 1–3 *Codiopsis lehmannae* sp. nov. BMNH EE5033, holotype; **1**, apical; **2**, oral; **3**, lateral; all × 4. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation.

Figs 4–7 *Actinophyma spectabile* Cotteau & Gauthier. BMNH EE3601; **4**, apical, × 3; **5**, oral, × 3; **6**, lateral, × 3; **7**, detail of ambital plating, × 6. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation.

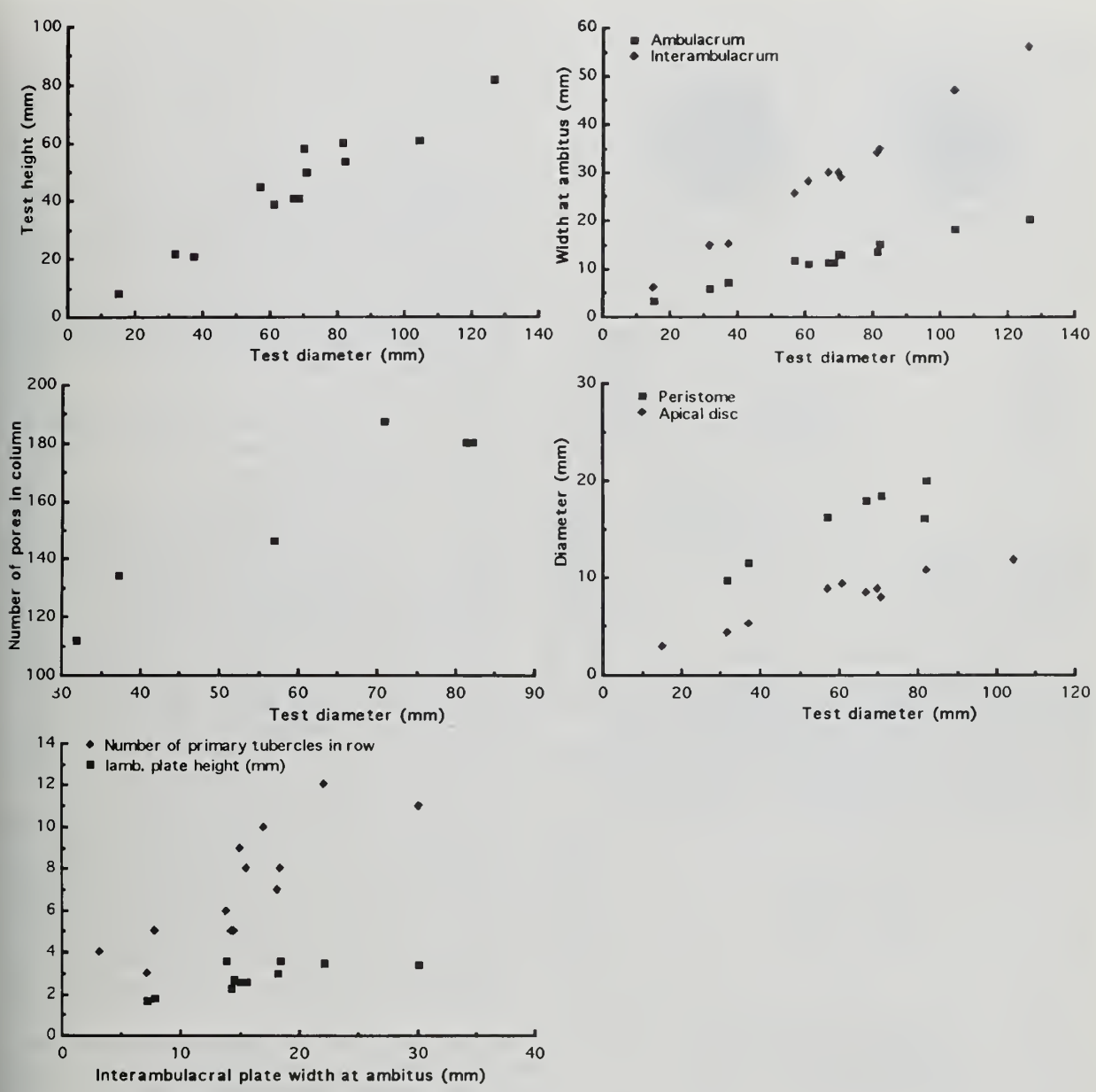


Fig. 29 Biometric data for *Noetlingaster paucituberculatus* (Noetling) and *N. emiratescus* Ali.

largest. These are arranged in a single, slightly arcuate row (Pl. 11, fig. 7), but the larger individuals may have two or three additional tubercles forming an upper row near the adradial suture. All tubercles are imperforate and non-crenulate and have relatively small mamelons and extensive areoles. Sutures between all plates are finely denticulate.

The peristome is very slightly sunken and is strongly indented by wide buccal notches. Peristome diameter is 20–31% of test diameter (mean = 27%, SD = 4·0%, N = 7).

Remarks. This species is distinguished from *N. emiratescus* by its interradial granular zone, which may be small and deveioped only adapically, or may be broad and extend adorally. Within a single population from bed 14, section 2, Jebel Rawdah, the development of this granular zone was highly variable, with some having only a narrow adapical wedge of granules, others having a broad band extending adorally. It also differs from *N. emiratescus* in having fewer interambulacral tubercles at comparable sizes (Fig. 28). Smaller individuals (diameters less than *ca.* 100 mm) have single rows of tubercles on interambulacral plates, but a second row is present in larger specimens.

The species was first described by Noetling (1897) on the basis of a single specimen from West Pakistan. Gauthier (1901) later described a smaller, incomplete specimen of this species under the name *N. monteili* from the eastern Sahara region of Algeria. Other species that are probably best treated as synonymous are the three species described by Checchia–Rispoli (1930) from the Maastrichtian of Libya.

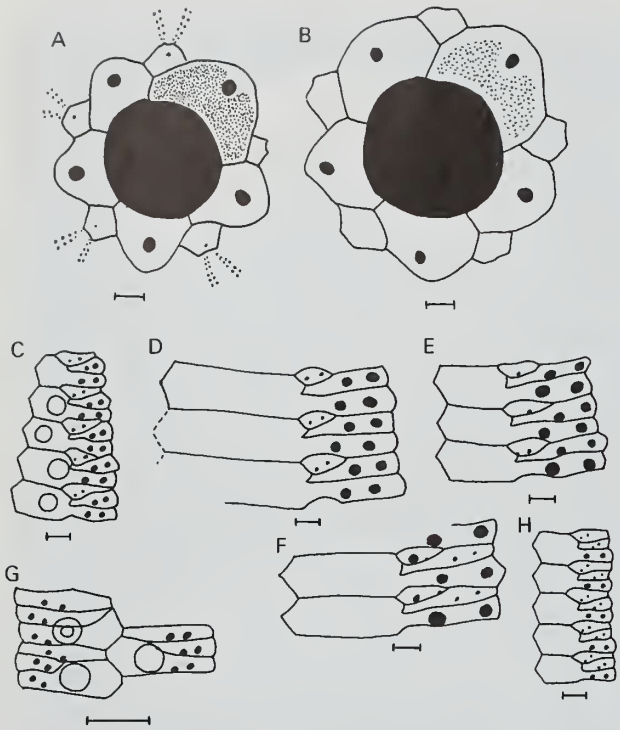


Fig. 30 Camera lucida drawings of *Noetlingaster*. **A-D, F, H,** *N. paucituberculatus* (Noetling): A, B, apical disc plating: A, BMNH EE3269; B, BMNH EE3275; C, adapical plating in a juvenile, BMNH EE5049; D, Ambital plating, BMNH EE3266; F, ambital plating, BMNH EE3286; H, adapical plating, BMNH EE3283. **E, G,** *N. emiratescus* Ali, BMNH EE3285; E, adapical plating; G, ambital plating. Scale bars = 1 mm.

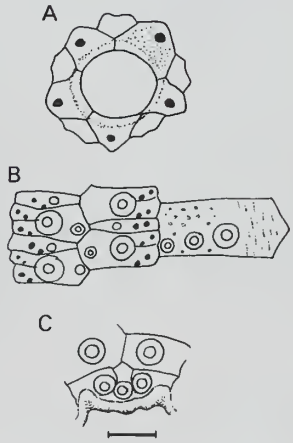


Fig. 31 Camera lucida drawings of plating in a juvenile *Noetlingaster paucituberculatus* (Noetling), BMNH EE3680. **A**, Apical disc; **B**, ambital plating, ambulacrum to the left, interambulcaral plate on right; **C**, adoral interambulacral plating, showing the single primordial interambulacral plate. Scale bar = 1 mm.

There is a general increase in size up the section at Jebel Rawdah, with small to medium-sized individuals found in the lower beds and only large individuals towards the top in the deeper water facies.

Noetlingaster emiratescus Ali, 1989 Pl. 11, figs 1–3; Figs 28, 29, 30E, G

1989 *Noetlingaster emiratescus* Ali: 398, Fig. 2 (3–5)

TYPES. The types of *N. emiratescus* are three specimens and six fragments in the collections of the Geology Department, United Arab Emirates University, Al Ain.

MATERIAL STUDIED. Three specimens, BMNH EE3279, EE3284–85.

OCCURRENCE. All specimens, including the type material, come from Jebel Rawdah. The specimens reported here were collected from bed 4, Jebel Rawdah section 1 (1) and bed 13, Jebel Rawdah section 4 (2).

DIAGNOSIS. A *Noetlingaster* with smaller and denser interambulacral tubercles than other species, and completely lacking a naked interradial zone.

DESCRIPTION. Tests range from 68·5 to about 105 mm in diameter. In outline the interradii and adradii are slightly depressed. Test height is 58–71% of test diameter and in profile the test is inflated and subglobular. The ambitus lies about one third of test height above the base.

The apical disc occupies 11% of the test diameter and has the same arrangement of plates as *N. paucituberculatus*. Ambulacral structure is also more or less identical, with the pore-pair on the occluded plate rudimentary almost to the apex (Figs 30E, G). The middle pore-pair is also rudimentary from the ambitus adorally. Ambulacral tubercles are irregularly arranged and occupy the full width of the ambulacra, one or two to a compound plate.

Interambulacral plates are slightly V-shaped, with a single well-developed row of tubercles along the lower edge and a second, irregular row of occasional tubercles above. There are 19 tubercles in a row at a test diameter of 71 mm, rising to 13 at 105 mm test diameter (Fig. 28). Tubercles occupy the full width of plates throughout and there is no granular interradial zone as is found in *N. paucituberculatus*.

The peristome is small and somewhat invaginated, occupying 26% of the test diameter.

REMARKS. Ali (1989) described this species on the basis of the material collected from Jebel Rawdah. Its small, numerous interambulacral tubercles and lack of any interradial zone of granulation serve to separate it from the co-occurring species, *N. paucituberculatus*.

Noetlingaster? sp. (juvenile?) Pl. 11, fig. 8; Fig. 27C

MATERIAL. One specimen, BMNH EE3689.

OCCURRENCE. From the *Loftusia* beds (beds 2–5), Jebel Huwayyah, section 2.

DIAGNOSIS. A species of arbaciid with a single primary interambulacral tubercle on ambital and adoral interambulacral plates, but smooth adapically. Ambulacral tubercles developed to apex. Broad ambital and adapical interradial zone ornamented with vertical riblets.

DESCRIPTION. The test is rounded pentagonal in outline and 13·2 mm in diameter. It has a broad flat base and domed

upper surface. Test height is 57% of test diameter and the ambitus lies at around 40% of test height.

The apical disc is 3·8 mm in diameter (29% of test diameter) and is dicyclic. It is not well preserved, but the genital plates are raised as a lip around the periproct margin and the periproct itself is 11% of the test diameter and oval in outline. Ocular plates protrude beyond the genital plates slightly.

Ambulacra are 20% of the test diameter in width at the ambitus. All plates are compound and trigeminate, but details of plate compounding are not clear. There is clearly a single element and a double element in each triad, but it is impossible to tell whether one of the double elements is a demiplate, as I suspect. All pore-pairs are equally well-developed. There is no phyllode development. There are 33 pore-pairs and 10 primary tubercles in a column.

Interambulacra are 39% of the test diameter in width at the ambitus. Each plate has a large adradial tubercle that extends adapically to within three or so plates of the apex. Adorally these tubercles lie subcentrally, but towards the apex they become positioned more and more closely towards the adradial suture. On ambital and adapical plates there is also a very much smaller mamelonate secondary tubercle lying at the centre of each plate within the zone of riblet ornamentation. The entire interradial zone from the ambitus upwards, has a well-developed ornamentation of vertically orientated riblets.

The peristome is 5·2 mm in diameter (40% of the test diameter) and is not invaginated. There are no raised interradial lips to the peristome margin. Buccal notches are extremely feeble.

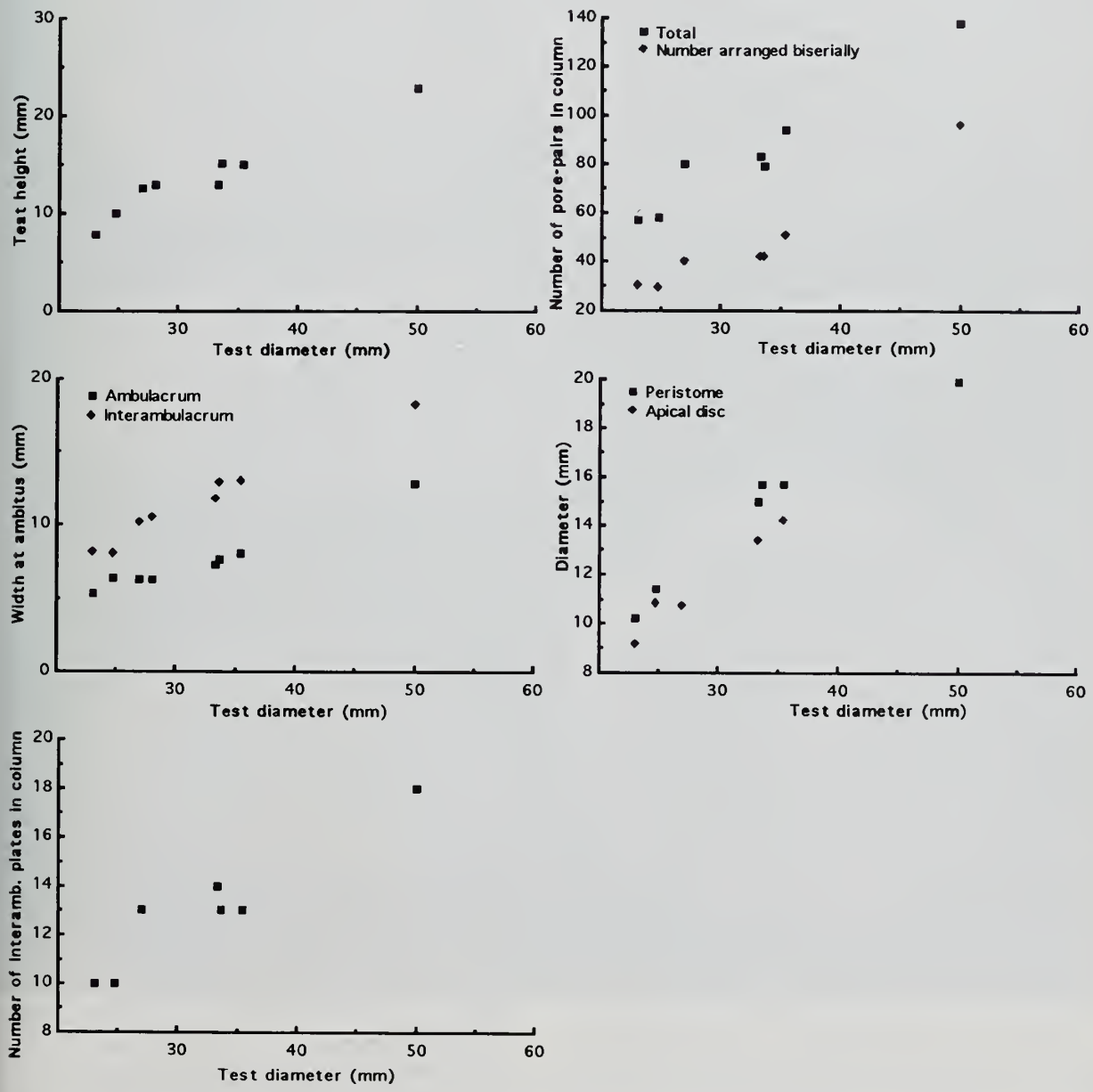


Fig. 32 Biometric data for *Phymosoma hexoaporum* Lambert.

REMARKS. This species is easily distinguished from *Hattopsis sphericus* on the basis of its interambulacral ornamentation of vertical riblets, and by its single row of primary interambulacral tubercles. It also lacks the reduced diameter pore-pair in each triad that is so characteristic of *H. sphericus* and *H. paucituberculatus*. It differs from *H. paucituberculatus* in its lower profile, less enlarged adapical pore-pairs and in its riblet ornamentation as opposed to the pitted ornamentation seen in *H. paucituberculatus* and *H. sphericus*. The vertical riblet ornamentation of *Noetlingaster?* sp. is characteristic of *Codiopsis* species such as *C. doma*, but *Noetlingaster?* sp. differs from *Codiopsis* in having no sharp reduction in the size of tubercles at the ambitus. It could possibly be the juvenile of a very much larger *Codiopsis* species, such as *C. stephensoni* Cooke, but it has open gonopores, which suggests that it is a genuinely small species. It differs from species such as *Codiopsis bruni* Lambert & Thièry (Maastrichtian of the Netherlands) and *C. disculus* Peron & Gauthier (late Campanian of Algeria, early Maastrichtian of Spain) in having a smooth, pustule-free upper surface. This specimen most likely represents a small *Noetlingaster*, one in which only the primary interambulacral tubercles have formed. However, neither of the named species of *Noetlingaster* shows the distinct vertical ribbing that characterises this specimen.

Order **PHYMOSOMATOIDA** Mortensen, 1904
Family **PHYMOSOMATIDAE** Pomel, 1883
Genus ***PHYMOSOMA*** Haime, *in* d'Archiac & Haime, 1853

Phymosoma hexoaporum Lambert, 1927 Pl. 13, figs 1–3; Figs 32, 33

1908 *Phymosoma (Cyphosoma) Archiaci* Cott. var: Cottreau: 21, pl. 3, fig. 1.
1927 *Phymosoma hexoaporum* Lambert: 35, pl. 2, figs 25–27.
1933 *Phymosoma Paronai* Checchia-Rispoli: 11, pl. 2, figs 4–7.

MATERIAL. Nineteen specimens of which the biometric data was drawn from the following: BMNH EE3607–08, EE3610–12, EE3614, EE3616, EE3618, EE3941.

OCCURRENCE. This species is found almost exclusively in the lowest beds of the Simsima Formation at Jebel Buhays, section 1 (16), and the immediately adjacent Jebel Thanais (3). In addition one specimen was found loose in the scree in Jebel Rawdah, section 3, and another in Bed 2 at Jebel Rawdah, section 4. Cottreau (1908) recorded an identical specimen from the late Cretaceous (?Maastrichtian) of Marohita, Eastern Madagascar.

DIAGNOSIS. A *Phymosoma* with a single large primary interambulacral tubercle on all plates, and one or two small adradial tubercles. Plates are composed of six or seven elements at the ambitus and pore-pairs are biserial from about the ambitus adapically. Interradial zones of small granules are very well developed.

DESCRIPTION. Tests range from 23 to 50 mm in diameter and are circular in outline. The test is depressed in profile (Pl. 13, fig. 3), with a height that is 34–46% of the test diameter (mean = 42%, SD = 4·4%, N = 8: Fig. 32). The ambitus lies slightly below mid-height.

The apical disc is caducous and is missing from all specimens. The outline of the apical disc is pentagonal with angles pointing interradially and projecting slightly further into the posterior interambulacrum (Pl. 13, fig. 2).

Ambulacra taper slightly both adapically and adorally. They measure 22–26% of the test diameter in width at the ambitus. All plates are polygeminate (Fig. 33). Above the ambitus pore-pairs are biserial and plates are composed of six to eight elements. Plate compounding is in the phymosomatid style. At the ambitus the pore-pairs are in arcs of six or seven in specimens more than 25 mm diameter, while subambitally they are quinquegeminate. Immediately adjacent to the peristome there are a couple of quadrigeminate plates. There are no sphaeridial pits adorally. Each compound plate carries a single large imperforate, crenulate tubercle, as large as the adjacent interambulacral primary tubercles. This occupies most of the plate. However, perradially there is a narrow band of small secondary and miliary tubercles (Pl. 13, fig. 3). Primary tubercles more or less reach the apex. There are 57–58 pore-pairs in a column at 23–24 mm test diameter, rising to 138 at 50 mm test diameter. Biserial pores appear immediately above the ambitus in most specimens and comprise 50–54% of the total number of pore-pairs in a column. In the very largest specimen, biserial pore-pairs extend to the subambital region.

Interambulacra are 32–38% of the test diameter in width at the ambitus. There are 10 plates in a column at 23 mm test diameter, rising to 18 at 50 mm test diameter (Fig. 32). Each plate carries a single large primary tubercle, centrally positioned. However, areoles are not contiguous, but are separated by a narrow band of miliary granules (Pl. 13, fig. 3). Tubercles are imperforate and crenulate and decrease in size gradually both adapically and adorally. There are one or two small secondary tubercles to each plate situated close to the adradial suture. In a few specimens these tubercles enlarge above the ambitus to about half the size of the primary tubercles, so as to form a secondary row. However, this is inconsistently developed. The interradius is broad and covered in scattered small secondary and miliary tubercles (Pl. 13, fig. 3). In some specimens (e.g. BMNH EE3614) this tuberculate band is relatively dense, whereas in other specimens (e.g. BMNH EE3618) tuberculation is more scattered. Both columns of plates reach the peristomial border.

The peristome is very slightly invaginated and occupies 40–47% of the test diameter. Buccal notches are small, but clearly incised (Pl. 13, fig. 1).

Lantern elements are seen scattered inside the test in BMNH EE3941. Hemipyramids are largely concealed by sediment, but one keeled tooth is seen in cross-section.

REMARKS. The variation encountered in the secondary tuberculation of this species is more marked than expected and is matched by a difference in the degree of tubercle crenulation. In the specimens with the denser miliary tuberculation interradially, there are usually well-developed secondary tubercles along the adradial margin in the region immediately above the ambitus, and primary tubercles are only weakly crenulate. In the more usual variety, the interradial zone has more scattered tuberculation, there is no enlarged secondary tuberculation and the primary tubercles have a well-developed and broad crenulate platform. These two forms may eventually prove to represent distinct species, but as they are both found at the same locality and the secondary tuberculation differences are not entirely consis-

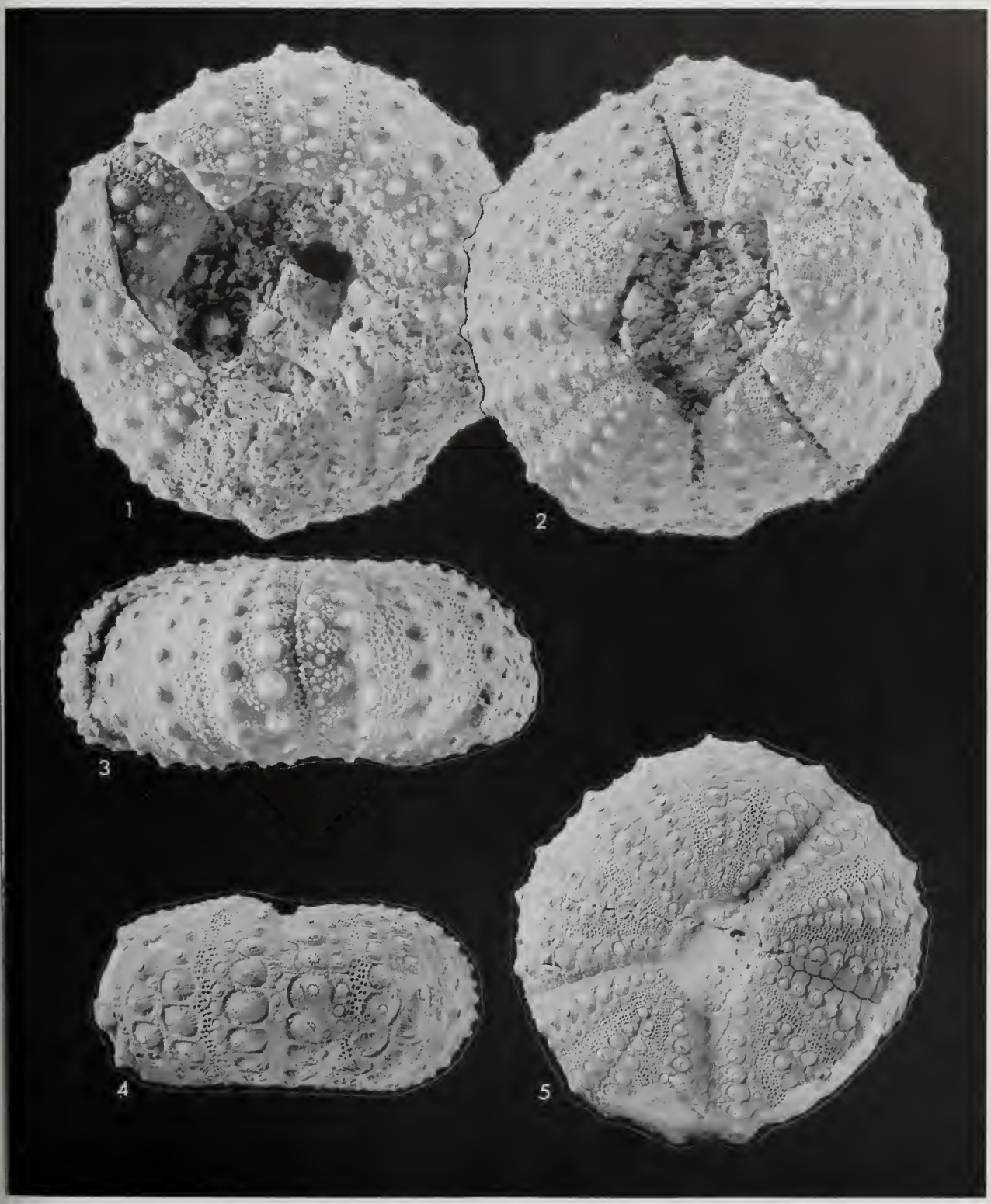


PLATE 13

Figs 1–3 *Phymosoma hexoaporum* Lambert. BMNH EE3614; **1**, oral; **2**, apical; **3**, lateral; all × 3. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation.

Figs 4, 5 *Actinophyma spectabile* Cotteau & Gauthier. B18731, Morgan Collection, Museum d'Histoire Naturelle, Paris; **4**, lateral; **5**, apical; both × 1·5. Senonian of Iran, no locality details.

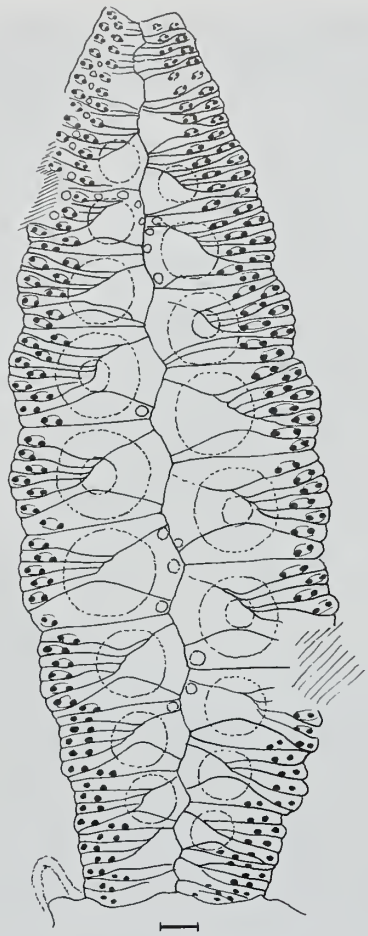


Fig. 33 Camera lucida drawing of ambulacral plating, from apex (top) to peristomial margin (bottom), in *Phymosoma hexoaporum* Lambert, BMNH EE3617. Scale bar = 1 mm.

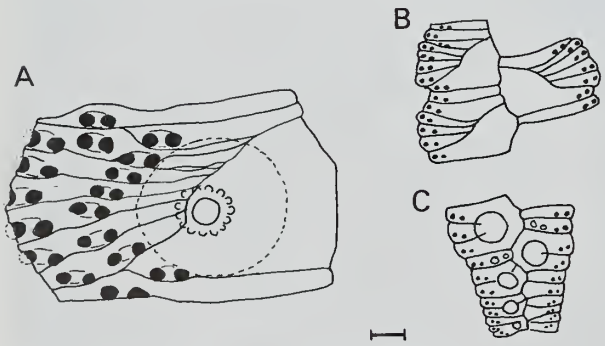


Fig. 34 Camera lucida drawings of plating in *Actinophyma spectabile* Cotteau & Gauthier. **A**, adapical ambulacral plate from a large individual, BMNH EE3599; **B**, supra-ambital ambulacral plating in a juvenile, BMNH EE3601; **C**, adoral ambulacral plating in a juvenile, BMNH EE3601. Scale bar = 1mm.

tent, the two forms are simply treated as varieties of the same species here.

The species described here appears identical to the specimen described from the Maastrichtian of Madagascar by Cottreau (1908) under the name *Phymosoma archiaci* Cotteau var. It differs from true *P. archiaci* in having a broader, more granular interradial zone, and in having less well-developed secondary tubercles on interambulacral plates. The species *P. hexoaporum* was established by Lambert (1927) for specimens from the Maastrichtian of Sopeira, province of Aragon, Spain. *P. hexoaporum* differed from all other species of *Phymosoma* described previously in having compound plates composed of six elements at the ambitus rather than five. Later, Checchia-Rispoli (1933) described the same species from the Maastrichtian of Libya under the name *P. paronai* Checchia-Rispoli. This too has six or seven elements in ambital ambulacral compound plates.

Genus *ACTINOPHYMA* Cotteau & Gauthier, 1895

Actinophyma spectabile Cotteau & Gauthier, 1895 Pl. 12, figs 4–7; Pl. 13, figs 4, 5; Fig. 34

1895 *Actinophyma spectabile* Cotteau & Gauthier: 98, pl. 25, figs 6–10.
1895 *Cyphosoma persicum* Cotteau & Gauthier: 93, pl. 25, figs 3–4.
1902 *Actinophyma spectabile* Cotteau & Gauthier; Gauthier: 151, pl. 20, figs 7–10.
1935 *Actinophyma spectabile* Cotteau & Gauthier; Mortensen: 489, fig. 287.

TYPES. The holotype is the specimen described by Cotteau & Gauthier from the upper Senonian of Endjir-kouh, Aftab district, Iran.

MATERIAL STUDIED. Six specimens, BMNH EE3598–3603, three of which are test fragments only. The following description is based on the two more or less complete specimens BMNH EE3601 (a juvenile) and BMNH EE3603 (an adult). Topotype material of *A. spectabile* in the Natural History Museum and in the Morgan Collection, Museum d'Histoire Naturelle, Paris, has been studied for comparison.

OCCURRENCE. Five of the specimens come from scree collections at Jebel Buhays, section 1 and are derived from the lowest few metres of the Simsima Formation. Two other specimens come from Jebel Rawdah section 3b, one from bed 8, the other from bed 9.

The species range is 'Upper Senonian' of southern Iran and Maastrichtian of the Oman Mountains.

DIAGNOSIS. A species of *Actinophyma* with strong radiating ridges on the boss of primary tubercles. Ambulacra polyploid adapically with up to 18 pore-pairs to an ambulacral plate arranged irregularly.

DESCRIPTION. Tests range in diameter from 21·2 mm to approximately 90 mm and are circular in outline. Test height is 33 mm in the larger specimen and 9·4 mm in the smaller (*ca.* 35–45% test diameter). In profile the ambitus is more or less at mid-height and is smoothly rounded below and slightly more conical above.

The apical disc is small; 5·8 mm diameter in the 21 mm individual (21% of test diameter) and probably only about 15 mm in the larger individual (16% of test diameter). Apical disc plates are lost from all specimens and were evidently not securely sutured to the corona. The opening is pentagonal in outline (Pl. 12, fig. 4; Pl. 13, fig. 5).

Ambulacra are almost as broad as the interambulacra, being 25·3 mm wide at the ambitus in BMNH EE3603, as compared to the interambulacral width of 28·7 mm. Pore-pairs are in arcs of six on the oral surface, becoming biserial subambitally in the larger specimen and continuing so to the apex (Fig. 34A). Adapical plates have up to 18 pore-pairs, and show phymosomatid-style compounding (Fig. 34A). In the small individual adapical pore-pairs are only just begining to become biserial and all plates have just six or seven elements (Pl. 12, fig. 7; Fig. 34B). There are 10 or so plates in a column at 21 mm diameter and 18 or 19 at 90 mm diameter. Each plate carries a single large primary tubercle that occupies most of the plate. However, in the larger individual there is a narrow adradial band of heterogeneous small secondary and miliary tuberculation. Ambulacral tubercles are not contiguous, but are separated by a band of small secondary tubercles. Areoles are strongly sculptured by radial grooves that extend from the base towards the platform of the boss.

The adoral plating in the small individual (BMNH EE3601) is noteworthy, since it comprises simple plating arranged in triads (Fig. 34C). However, standard phymosomatoid-style compounding develops subambitally, and this appears to be simply a juvenile feature.

There are 11 interambulacral plates in a column at 21 mm test diameter, rising to about 18 at 90 mm test diameter. Each plate carries a large primary tubercle with a small imperforate mamelon and a crenulate platform. Areoles at the ambitus and adorally are confluent and are oval in outline. The areole bears strong radial grooves which extend up the sides of the boss (Pl. 12, figs 5, 6). These are most pronounced in the smaller individual. Tubercles decrease in size above the ambitus. The primary tubercles are centrally positioned on the plate and there are relatively broad adradial and interradial bands of secondary tuberculation. On plates around the ambitus there is an enlarged secondary tubercle to the adradial side of the primary tubercle, but otherwise secondary tuberculation is small and heterogeneous. The interradial zone is depressed and tubercle-free towards the apex.

The peristome is relatively small and invaginated. In the 21 mm individual it is 7·1 mm in diameter (33% of test diameter), and is proportionally smaller in the larger individual. Buccal notches are very shallow (Pl. 12, fig. 5).

Remarks. When first erected (Cotteau & Gauthier, 1895), this species was based on a small individual 29 mm in diameter, which is virtually identical to BMNH EE3601 in morphology. In the same publication Cotteau & Gauthier (1895: 91) erected another species, *Cyphosoma persicum* on the basis of a larger, but fragmentary specimen from Derre-i-Chahr. Subsequently, with the collection of more material, Gauthier (1902) recognized that *A. spectabile* and *C. persicum* were simply different growth stages of the same species and synonymized the two, selecting *A. spectabile* as the valid name.

The characteristic radial striation, which is so strongly evident in juveniles, makes this an easily recognizable species. Only one other comparable species has been described, *Actinophyma* cf. *A. spectabile* Kier (1972: 68), from the Campanian of Saudi Arabia. This differs from the Iranian and Omani species in having deep pits developed at the corners of interambulacral plates on interradial sutures.

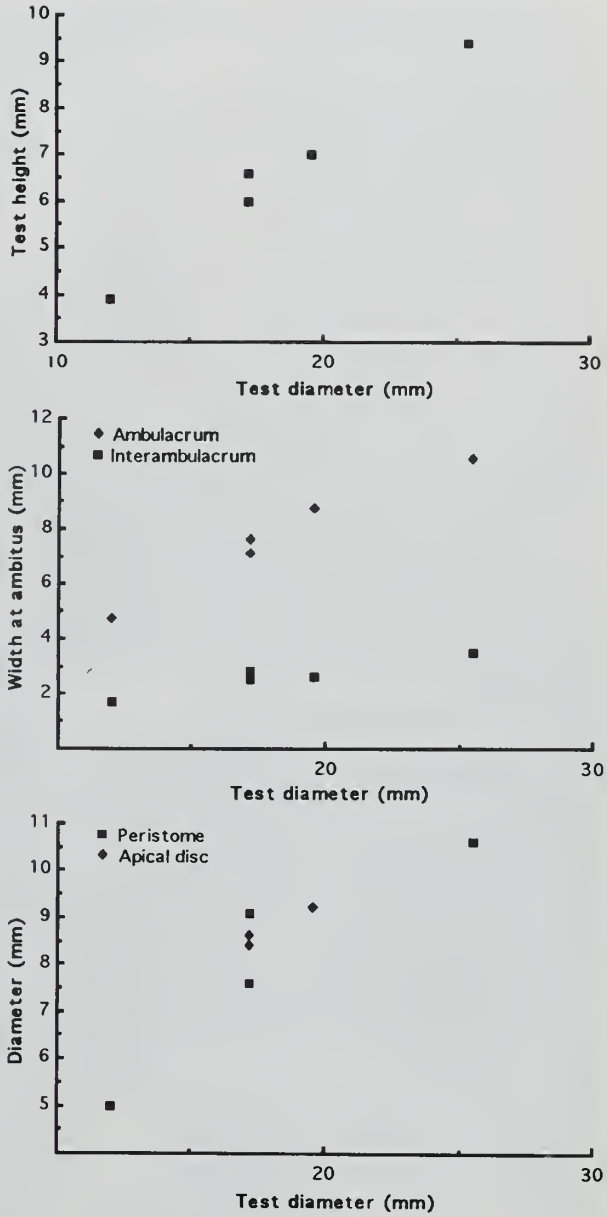


Fig. 35 Biometric data for *Plistophyma asiaticum* Cotteau & Gauthier.

Genus ***PLISTOPHYMA*** Peron & Gauthier, *in* Cotteau, Peron & Gauthier, 1881.

Plistophyma asiaticum Cotteau & Gauthier, 1895Pl. 14, figs 1–7; Figs 35, 36

1895 *Plistophyma asiaticum* Cotteau & Gauthier: 105, pl. 16, figs 11–14.

Types. The holotype is the single specimen described and figured by Cotteau & Gauthier. It is not in the Morgan collection in the Museum d'Histoire Naturelle, Paris.

Material studied. Six specimens, BMNH EE3572–76, EE4932. Only BMNH EE3573, which is incomplete, was

omitted from the biometric analysis given below.

OCCURRENCE. In the western Oman Mountains this species was found at the following levels and localities:
Jebel Buhays, section 1: loose in scree, derived from lowest few metres of the Simsima Formation (4).
Jebel Thanais: From the lowest metre of Simsima Formation (2).
Jebel Rawdah, section 2, bed 4 (1).

The species was described from the Senonian of Derre-i-Chahr, southern Iran and there are no other records.

DIAGNOSIS. A *Plistophyma* in which the ambital interambulacral plates are very much smaller and narrower than either adoral or adapical plates.

DESCRIPTION. Tests range in diameter from 12 to 25·5 mm and are rounded pentagonal in outline with the angles interradial. Tests are depressed and rounded in profile, with the ambitus at or very slightly below mid-height (Pl. 14, figs 3, 4). Test height is 33–38% of test diameter (mean = 36%).

The apical disc is large and pentagonal in outline with the angles interradial (Pl. 14, fig. 2). It is 47–50% of the test diameter in diameter and is not invaginated. No specimen retains any apical disc plates but, to judge from the size and shape of the opening, disc plating was presumably monocyclic.

Ambulacra are 13–16% of the test diameter in width at the ambitus. They are narrowest ambitally and expand slightly adapically (Fig. 36A). Plates both at the ambitus and adorally are trigeminate with all three elements reaching the perradial suture (Fig. 36C). The central element is the largest. Each plate carries a single imperforate, non-crenulate tubercle which straddles all three elements. Adorally, pore-pairs become crowded so as to form small phyllodes (Pl. 14, fig. 6). Immediately above the ambitus pore-pairs become biserially arranged and primary tubercles diminish in size and do not reach the apex (Pl. 14, fig. 5). There are 48 pore-pairs in a column (of which the most adapical 18–20 are biserially arranged). There are 12 or 13 primary tubercles. Secondary tubercles lie immediately adjacent to each pore-pair and may also occur along the perradius on occasional elements.

Interambulacra are 39–44% of the test diameter in width at the ambitus. Each plate is very wide and short and bears a row of small, equal-sized tubercles. These are imperforate and appear non-crenulate, but on close inspection of well-preserved material (e.g. BMNH EE3573) there are faint traces of crenulation to larger tubercles. At the ambitus the interambulacral plates become very much narrower and the size of the tubercles more or less halves (Pl. 14, figs 3, 4; Fig. 36B). All plates are arranged to form a pronounced downward-pointing V. Both columns of plates reach the peristomial border. The peristome is 42–52% of the test diameter in diameter and is hardly invaginated. There are very feeble buccal notches. The perignathic girdle consists of small auricles which do not meet above the perradius.

REMARKS. The species is distinguished from the type species *P. africanum* Peron & Gauthier (Cotteau *et al.* 1881) by its somewhat sharper decrease in interambulacral plate size at the ambitus. However, the two species are very similar indeed in other features and the Algerian and Omani-Iranian species may eventually turn out to be conspecific. The residual crenulation on well-preserved tubercles and the large

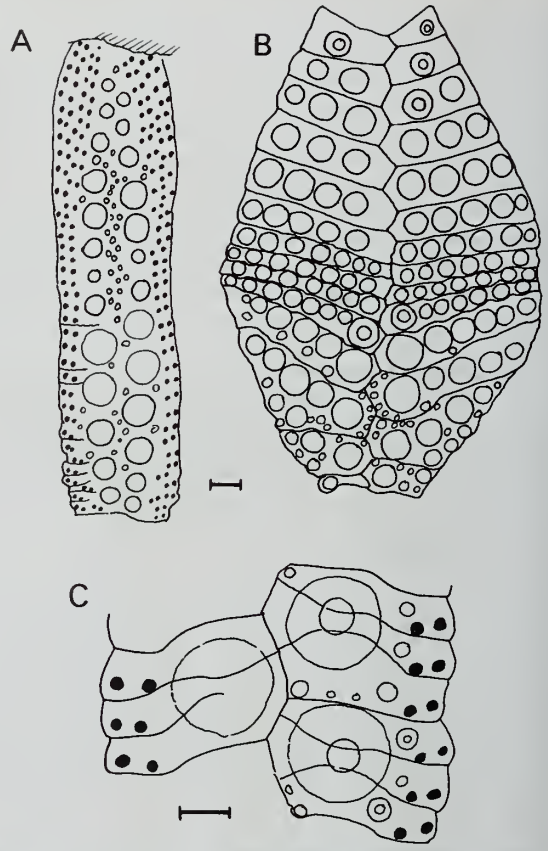


Fig. 36 Camera lucida drawings of plating in *Plistophyma asiaticum* Cotteau & Gauthier, BMNH EE3575. **A**, ambulacrum, from apex (top) to peristomial margin (bottom); **B**, interambulacrum from apex (top) to peristomial margin (bottom); **C**, detail af ambital ambulacral plating. Scale bars = 1 mm.

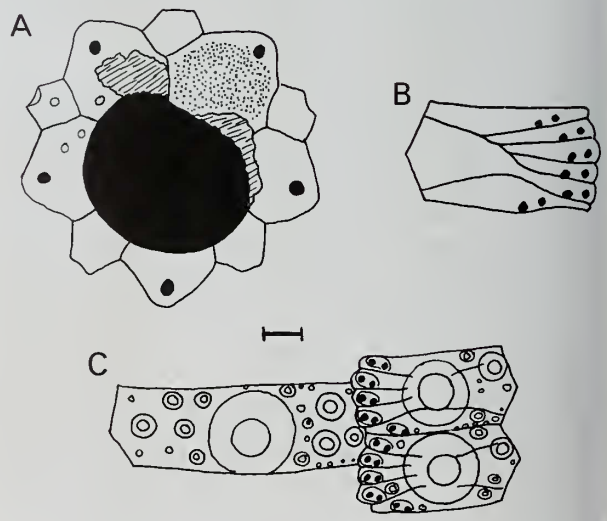


Fig. 37 Camera lucida drawings of plating in *Circopeltis? emiratus* sp. nov. **A**, apical disc, BMNH EE3584; **B** ambital ambulacral plating, BMNH EE3582; **C**, ambital plating, ambulacrum to right, interambulacral plate to left, BMNH EE3584. Scale bar = 1 mm.

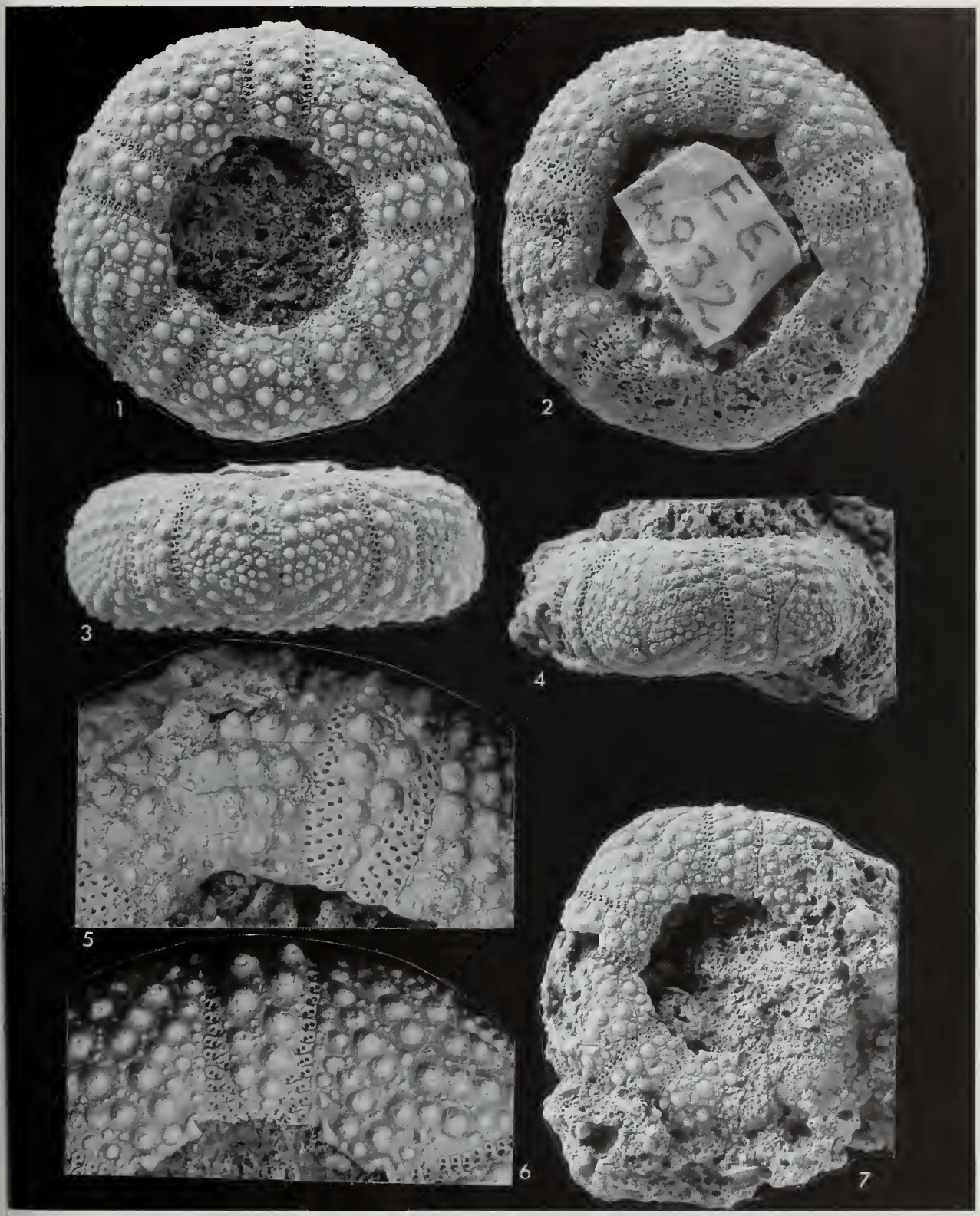


PLATE 14

Figs 1–7 *Plistophyma asiaticum* Cotteau & Gauthier. **1–3, 6**, BMNH EE4932; **1**, oral, × 5; **2**, apical, × 5; **3**, lateral, × 5; **6**, detail of peristomial region, × 8. Jebel Thanais, lowest 1 m of the Simsima Formation. **4, 7**, BMNH EE3575; **4**, lateral; **7**, oral; both × 3. Jebel Thanais, basal 1 m of the Simsima Formation. **5**, BMNH EE3572; apical detail, × 8. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation.

pentagonal caducous apical disc suggests that *Plistophyma* belongs within the phymosomatoids.

Family **STOMECHINIDAE** Pomel, 1883
Genus ***CIRCOPELTIS*** Pomel, 1883

Circopeltis? emiratus sp. nov. Pl. 15, figs 1–3; Pl. 17, figs 1, 2; Fig. 37

TYPES. The holotype is BMNH EE3584 and paratypes are BMNH EE3582, EE3583, EE3585 and EE3596.

OTHER MATERIAL. There is one other fragment tentatively attributed to this species, BMNH EE3586.

OCCURRENCE. In the western Oman mountains this species is found at the following levels:
Jebel Buhays section 1: loose in scree (derived from lower beds of the Simsima Formation) (1).
Jebel Buhays section 3: immediately overlying prominent red marly sand level (*ca.* 3 m above the base of the Simsima Formation) (2).
Jebel Rawdah section 3: bed 6 (1). Section 3b basal 1 m (1).
Jebel Rawdah, section 4: bed 4 (1).

It is thus known from the Maastrichtian of the western Oman Mountains.

DIAGNOSIS. Test low, domal; apical disc hemicyclic with plates firmly bound to the corona. Ambulacra straight, plating compound in the phymosomatoid style with five or six elements to a compound plate; pore-pairs arranged in arcs from apex to peristome. There is a single large primary tubercle to each plate with broad adradial and interradial zones of secondary tuberculation.

DESCRIPTION. Tests range in diameter from 20·1 mm to 47·2 mm and in height from 11·8 to 23·5 mm (mean test height is 53% of test diameter). The test is circular in outline and flattened ovate in profile, with the ambitus at approximately 40% of test height above the base.

The apical disc is hemicyclic, with the three anterior oculars insert and the posterior two exsert (Fig. 37A). The apical disc is 19–24% of the test diameter in diameter (mean = 22%) and the periproct occupies approximately 55% of the apical disc diameter. The periproct is D-shaped in outline, with the slightly flattened edge abutting the madreporite. Genital plate 2 is the largest and is tumid and covered in dense madrepores. Other genital plates and all ocular plates have a scattering of small miliary tubercles.

The ambulacra are 22–24% of the test diameter in width at the ambitus. They are straight and taper gradually adapically. All plates are compound in the phymosomatid style (Fig. 37B) and most are composed of five, or occasionally six, elements. The three most adoral plates however are composed of just four elements. Pore-pairs are arranged in arcs and phyllodes are developed around the peristomial edge. Each compound plate has a single large primary tubercle (imperforate and non-crenulate) that overlaps all five (or six) elements that make up the compound plate (Fig. 37C; Pl. 17, fig. 1). There is a much smaller secondary tubercle lying perradially, plus one or two scattered miliary granules. The perradial zone is relatively broad. There are 14 compound plates and 73 pore-pairs at 20 mm test diameter, rising to 18 compound plates and 88 pore-pairs at 37 mm test diameter. There are no sphaeridial pits.

Interambulacra are broad and carry two rows of primary tubercles, set close to the adradial margin. There are 13 plates in a column at 20 mm test diameter, rising to 17 at 37 mm test diameter. Areoles are almost contiguous adorally but are separated adapically. The mamelon is large and imperforate and there is a narrow ledge that may retain faint traces of crenulation in well-preserved individuals. Adradially there is a narrow band of small secondary tubercles and miliary granules. Interradially the plates are slightly depressed and there are small and irregularly scattered secondary tubercles throughout (Pl. 17, fig. 2). Both columns reach the peristomial margin.

The peristome is about 42% of the test diameter across. It is slightly invaginated. Buccal notches are moderately well-developed and have a thickened lip. Lantern and spines are unknown.

REMARKS. This species has a phymosomatid style of ambulacral compounding. However, the apical disc structure differentiates it from the great majority of phymosomatids, since these almost all have monocyclic apical discs that are typically caducous. Only *Glyptocidaris* has a comparable apical disc. Furthermore, this species has tuberculation that is virtually non-crenulate, whereas other genera, including *Glyptocidaris*, show stronger crenulation. The species is here tentatively assigned to the genus *Circopeltis*. *Circopeltis* has polygeminate plate compounding and a hemicyclic apical disc. *Circopeltis* also has non-crenulate tuberculation. However, its ambulacral compounding style is unreported and it is not yet known whether it is phymosomatoid.

It differs from *Phymechinus? perplexus* in its finer tuberculation, with more extensive scattered secondary tuberculation. More importantly it has ambulacral pore-pairs in simple arcs throughout. In *Phymechinus* pore-pairs become irregularly biserial adapically. Furthermore, *Circopeltis?* has a larger peristome and much less well developed phyllodes than does *Phymechinus? perplexus* from the same levels. However, there is little doubt that the two forms are rather closely related.

Genus *PHYMECHINUS* Desor, 1856

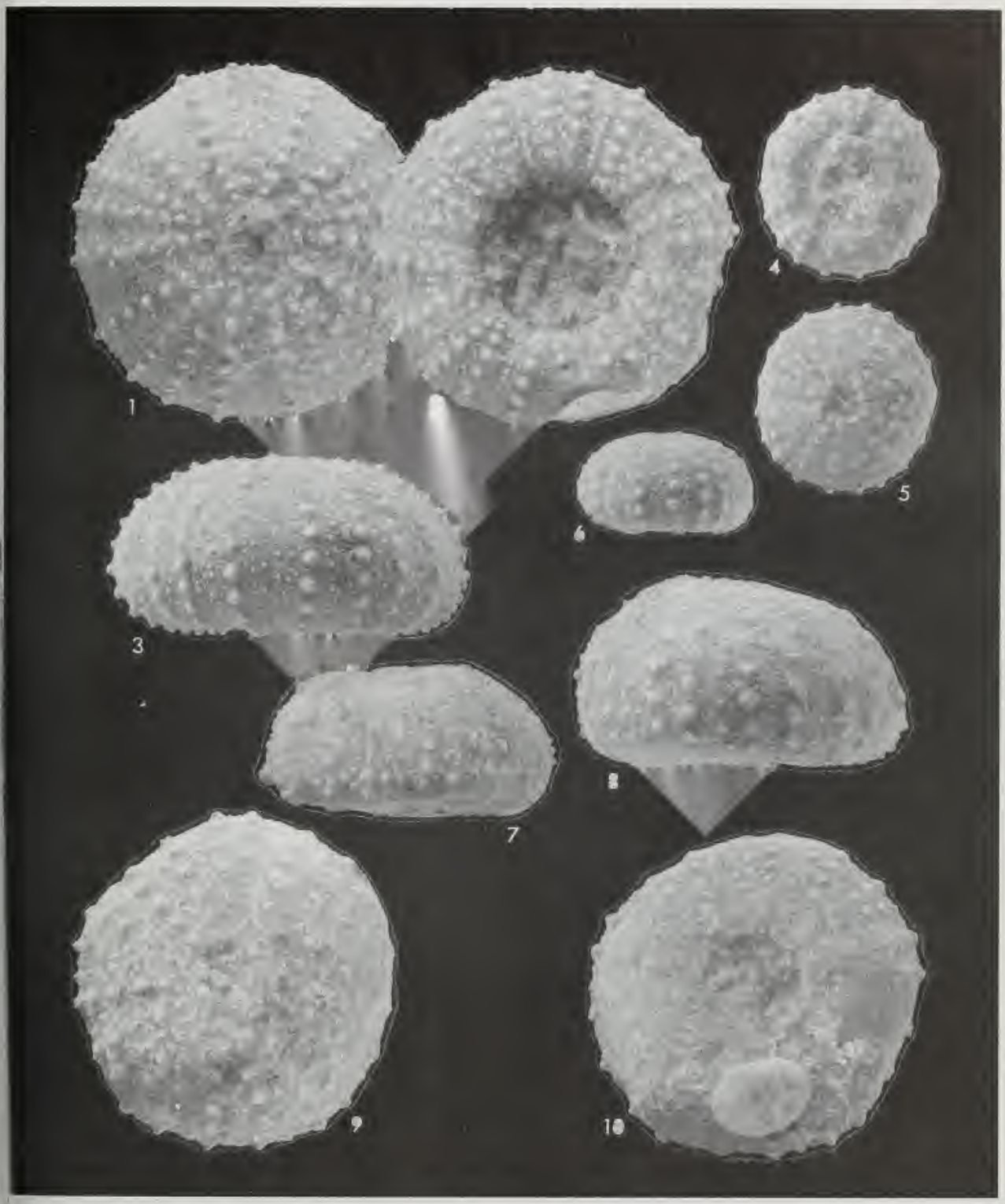
Phymechinus? perplexus sp. nov Pl. 15, figs 4–10; Figs 38, 39

TYPES. Holotype EE3579, paratypes BMNH EE3581, EE3591, EE3593, EE3619.

MATERIAL STUDIED. 14 specimens, of which biometric data was derived from the following: BMNH EE3578–79, EE3581, EE3989, EE3991–94, EE3619.

OCCURRENCE. All specimens come from Jebel Rawdah as follows:
Section 1: bed 4 (2).
Section 2: bed 6 (2); bed 8 (4); bed 11 (1); loose in scree (4).
Section 4: bed 8/9 (1).

DIAGNOSIS. Apical disc small, caducous. Ambulacra polygeminate with seven or eight elements to a compound plate. Plate compounding phymosomatid-style. Pore-pairs arcuate or irrgularly multiple above. One primary imperforate, crenulate tubercle on each ambulacral and interambu-


1
2
3
4
5
6
7
8
9
10

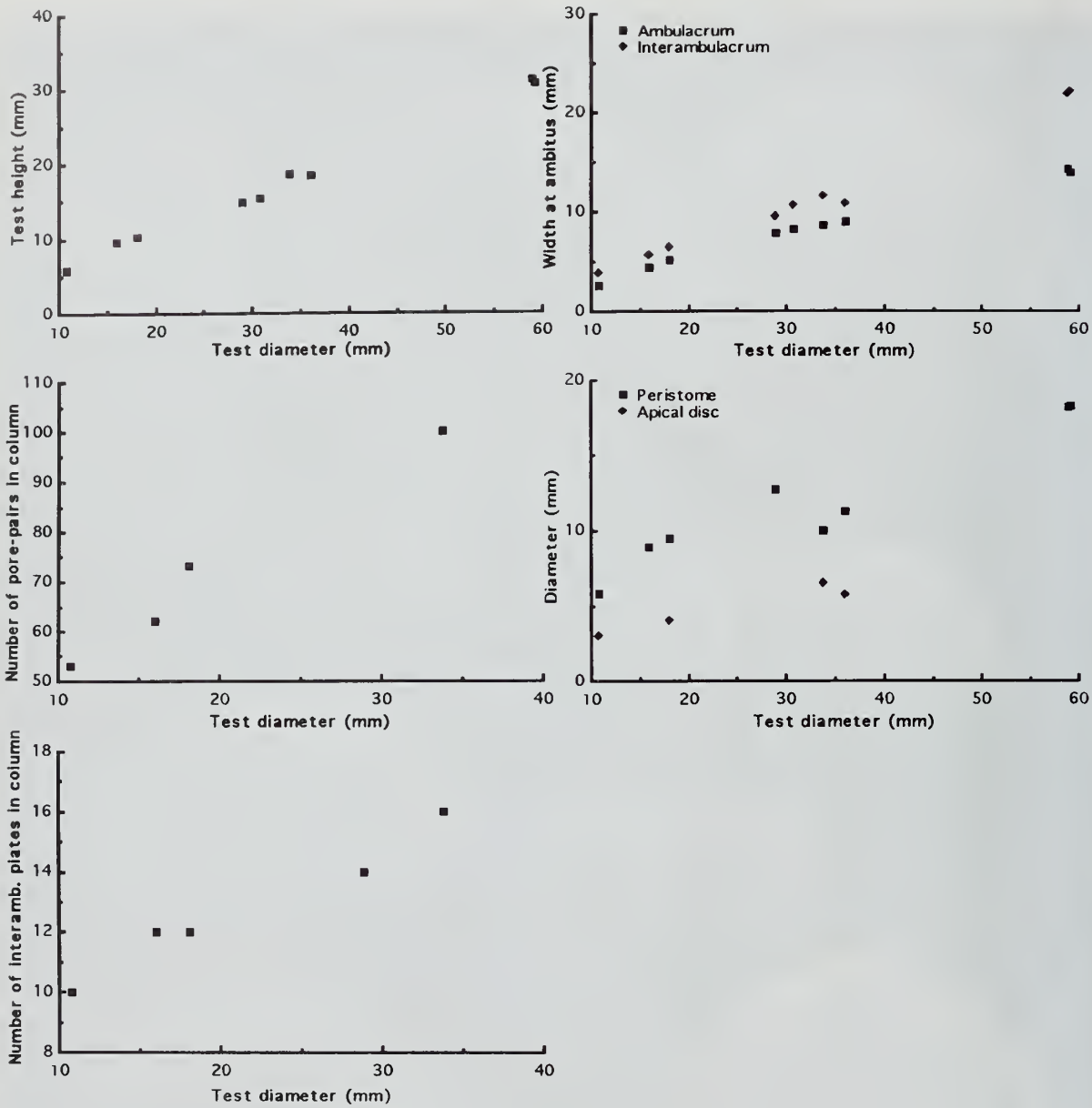


Fig. 38 Biometric data for *Phymechinus? perplexus* sp. nov.

lacral plate. Mamelons very large and crenulation feebly developed. Lower surface flat, peristome small with feeble buccal notches. Phyllodes extremely well-developed.

DESCRIPTION. Tests are 11 to 60 mm in diameter and 5·8 to 31·2 mm in height (test height 50–60% of diameter; mean = 54%, SD = 3·2%, N = 9). They are circular in outline and bun-shaped in profile, with a broad base and depressed conical upper surface (Pl. 15, fig. 8). The ambitus lies at approximately 30% of test height above the base.

The apical disc is small and circular, only 16–28% of the test diameter across (Pl. 15, fig. 9). It is proportionally smaller in larger individuals (Fig. 38). No specimen retains any apical disc plating, but to judge from the small size of the opening, plating is almost certain to have been dicyclic or hemicyclic.

Ambulacra are only slightly narrower than interambulacra at the ambitus and measure 23–28% of the test diameter in width (mean = 25·5%, SD = 1·8%, N = 9). They are more or less straight, tapering slightly adorally and more significantly adapically. All plates are polygeminate with seven (rarely six or eight) pore-pairs to an ambital plate. Plate compounding is in the phymosomatid style (Figs 39A, B). Pore-pairs are strongly arced at the ambitus, but tend to become irregularly biserial or pleuriserial adapically and adorally (Figs 38C, D). Close to the apex, pore-pairs once again become uniserially arranged. Adapically, small secondary tubercles occur scattered within the pore zone. However,

there are a few specimens (e.g. EE3581) in which the pore-pairs are in uniserial arcs right to the apex. Each plate carries a single large primary tubercle that occupies most of the plate (Pl. 15, fig. 7; Figs 38A, B). This has a relatively well-developed imperforate mamelon and is distinctly crenulate, though the surrounding platform is not very broad. Areoles are circular and separated by a single ring of small secondary and miliary tubercles. There are 53 pore-pairs in a column at 11 mm test diameter, rising to about 100 pore-pairs at 34 mm test diameter (Fig. 38). Tubercles are largest at the ambitus and decrease in size gradually both adapically and adorally. Adorally there are very strong phyllodes composed of circular pore-pairs with well-developed periporal muscle attachment areas (Pl. 15, fig. 10). These phyllodes are so large as to make up more than half of the ambulacral width.

Interambulacra are relatively narrow, being only 30–37% of the test diameter in width at the ambitus. There are 10 plates in a column at 11 mm test diameter, rising to 16 at 34 mm test diameter. Each plate carries a large primary tubercle which is imperforate and weakly crenulate. In smaller specimens (i.e. less than 35 mm) these are the only large tubercles present, although a distinct small secondary tubercle is present both adradially and interradially. In specimens around 58 mm test diameter the adradial secondary tubercle reaches approximately half the diameter of the primary tubercle at the ambitus and adorally, and there are additional smaller secondary tubercles close to the adradial suture. Primary and secondary tubercles extend to the apex and peristome. The primary tubercles are non-confluent, being separated by a single row of miliaries.

The peristome is 30–55% of the test diameter in width (proportionally smaller in larger individuals) and is hardly invaginated, the entire lower surface being flat. Buccal notches are small and poorly developed. Spines, lantern and pedicellariae are all unknown.

Remarks. It is with some slight hesitation that I refer the new species *P? perplexus* to this genus. This species has stout tubercles with large mamelons and virtually no platform. Nevertheless fine crenulation is developed around the mamelon, though it is often difficult to see unless preservation is near perfect. The ambulacral plate compounding is phymosomatid in style, with adapical pore-pairs either strongly arcuate or, more often, actually multiple in an irregular way. The apical disc is small and unlikely to be monocyclic, but plating is not preserved. The type species of *Phymechinus*, *P. mirabilis* (Agassiz) comes from the Middle Oxfordian and has a similar overall shape, small apical disc and stout tuberculation. Well-preserved specimens (e.g. Hess 1975, pl. 37, fig. 5) apparently show feeble crenulation. Unfortunately, none of the specimens I have examined show the style of ambulacral compounding. *P? perplexus* differs from the type species in having a proportionally smaller peristome and better developed phyllodes. It also has much less well-developed buccal notches. In tuberculation style it is very similar to Schluter's species *Phymechinus cretaceus* from the *B. mucronata* Zone, Upper Campanian of Ciply, Belgium, but this species has a much larger peristome and much less well-developed phyllodes. This species is easily distinguished from *Phymosoma* cf. *paroni* Checchia-Rispoli by its very much smaller apical disc, more subconical profile and compound amulacral plates that incorporate more than five elements. It is also easily distinguished from *Actinophyma*. Although *Actinophyma* has a similar arrangement of pore-pairs adapically, forming rather irregular multiple columns with intersperced tubercles, it is very different adorally. The peristome in *Actinophyma* is invaginated and the pore-pairs remain uniserial and rather widely spaced across the entire oral surface. In *P? perplexus* the pore-pairs form a very strong phyllode and the oral area is broad and flat.

It is distinguished from *Circopeltis emiratus* by its very much coarser tuberculation, smaller peristome, more polygeminate ambulacral compounding and cadoucous apical disc. Furthermore, *C. emiratus* never developed biserial pore-pairs adapically.

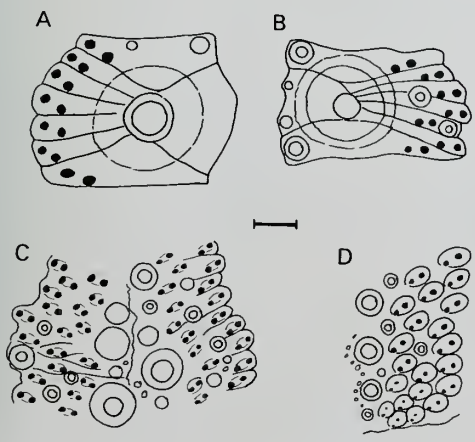


Fig. 39 Camera lucida drawings of plating in *Phymechinus? perplexus* sp. nov., BMNH EE3581. **A**, ambital ambulacral plate; **B**, adapical ambulacral plate; **C**, adapical pore-pair arrangement; **D**, adoral pore-pair arrangement. Scale bar = 1 mm.

Genus ***ECHINOTIARA*** Pomel, 1883

Echinotiara perebaskinei Lambert, 1930 Pl. 16, figs 1–6; Pl. 17, figs 3, 6, 7; Figs 40, 41

1930 *Echinotiara perebaskinei* Lambert, in Lambert & Perebaskine: 472, pl. 38, figs 1–5.

Types. The two specimens figured and described by Lambert and presumably in the Lambert Collection, Université de Paris VI, France.

Material studied. 82 specimens of which only the following were used in the biometric analysis: BMNH EE3756–57, EE3761–63, EE3767–69, EE3772, EE3774, EE3782, EE3785–88.

Occurrence. Along the western margins of the Oman mountains this species is confined to the lowest arenaceous levels of the Simsima Formation at Jebel Rawdah. It occurs as follows:

Jebel Rawdah, section 2: bed 4 (6); bed 6 (9); bed 8 (49); bed 11 (3); loose in lower scree (17).
Jebel Rawdah, section 3b: bed 3 (1).
Jebel Rawdah, section 4: bed 2 (1); bed 8/9 (1).

The species was originally described from the 'Calcaires inferieur a *Libycoceras*, Maastrichtien' at Oued Tarinkat, Tchi-Dermine and Oued Tinamassine in the district of Gao,

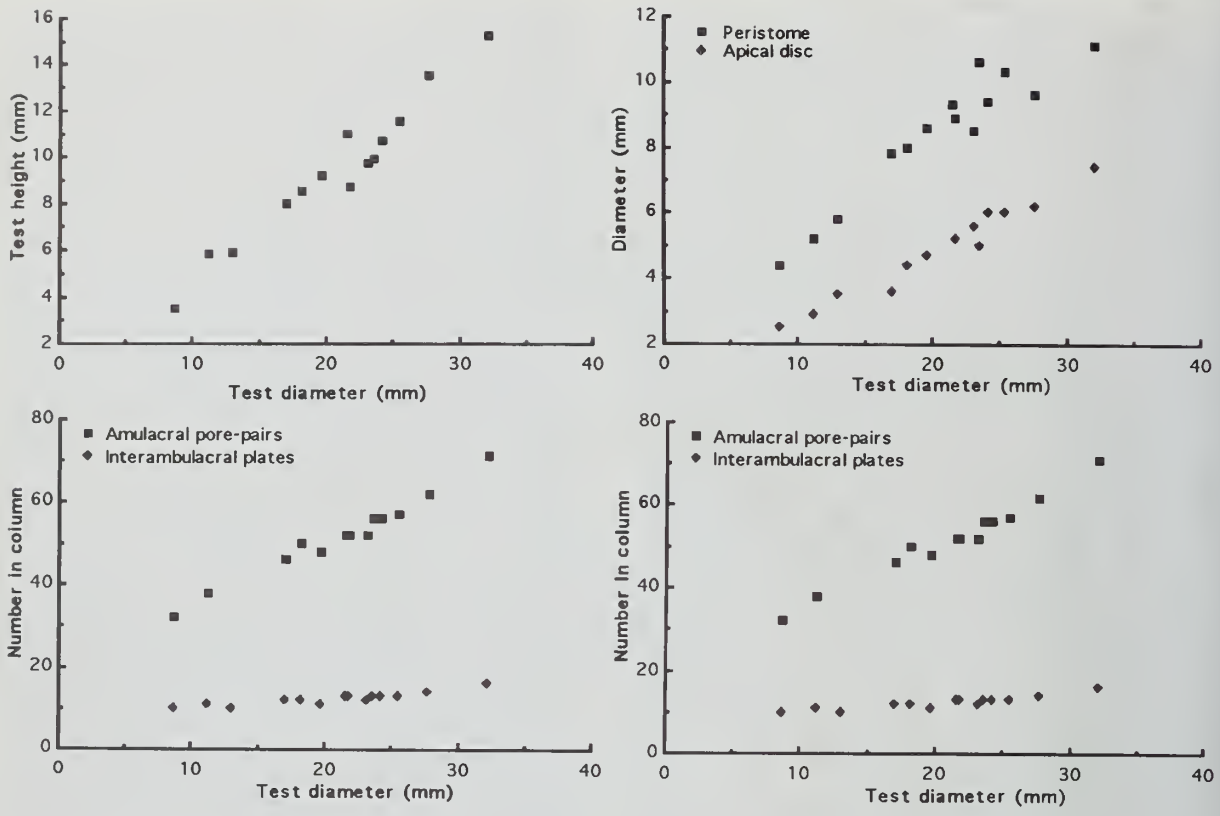


Fig. 40 Biometric data for *Echinotiara perebaskinei* Lambert.

Niger (Lambert & Perebaskine 1930). Amard *et al.* (1981: 124) reported an *Echinotiara* cf. *perebaskinei* Lambert from the Upper Maastrichtian of Tademait, Algeria, but as no figures or description are given it is not possible to confirm this record.

DIAGNOSIS. An *Echinotiara* with a relatively small caducous apical disc, ambulacral pore-pairs in arcs of three, with very strong phyllodes developed adorally. Interambulacral plates with a single large primary tubercle and well-developed adradial and interradial secondary tubercles that diminish in size adapically.

DESCRIPTION. Tests range from 9 to 32 mm in diameter and are more or less circular in outline. Test height is 40–52% of test diameter (mean = 46%, SD = 3·7%, N = 14). In profile the test is low conical (Pl. 16, fig. 3), with the ambitus approximately 40% above the base.

The apical disc is always missing and plating can only have been loosely fixed to the corona. The apical disc outline is irregularly circular (Pl. 16, fig. 1) and is 21–29% of the test diameter in length (mean = 24%, SD = 2·1%, N = 13). To judge from the size, it must have been dicyclic or hemicyclic.

Ambulacra are trigeminate throughout with pore-pairs arranged in distinct arcs of three (Fig. 41A). Ambulacra are relatively broad, being approximatley 22% of the test diameter in width at the ambitus. They taper gradually adapically, but primary tubercles continue to the apex (Pl. 17, fig. 3). Adorally the ambulacra remain broad and there are large, well-developed phyllodes, which in specimens 25 mm in diameter include at least 22 pore-pairs in each column (Pl. 16, fig. 5). Each compound plate carries a single large imperforate and non-crenulate tubercle that overlaps all three elements (Fig. 41). Plate compounding is diadematoid in style, with all three elements reaching the perradius and the middle plate pinched towards the centre of the plate (Fig. 41C). The lowest element in each compound plate carries a small secondary tubercle adradially and perradially. There are 32 pore-pairs in a column at 9 mm test diameter, rising to 71 at 32 mm test diameter (Fig. 40).

At the ambitus the interambulacra are 35–38% of the test diameter in width. Both columns reach the peristomial border, although the interambulacra taper considerably towards the peristome. Plates at the ambitus are longer than wide and are slightly curved. Each plate carries a single large imperforate and apparently non-crenulate tubercle at its centre (Pl. 17, fig. 7). The mamelon is slightly undercut but there is little surrounding platform developed. On the adradial side there are one or two smaller secondary tubercles, while on the interradial edge there is a single secondary tubercle (Fig. 41C). These primary and secondary tubercles are relatively coarse and occupy most of the available space. There are, however, miliary granules and small tertiary tubercles along the adapical margin and in spaces adjacent to the primary tubercle. There are 10 plates in a column at 9 mm test diameter, rising to 16 at 32 mm test diameter. Primary tubercles continue to the apex and there is no median naked zone.

The peristome is circular and measures 35–50% of the test diameter in diameter (it is proportionally larger in smaller individuals (Pl. 16, figs 4, 5). It is only slightly sunken and

PLATE 16

Figs 1–6 *Echinotiara perebaskinei* Lambert. Jebel Rawdah, section 2, beds 6–8. **1, 2,** BMNH EE3756; **1**, apical, **2**, oral; both × 3. **3, 4,** BMNH EE3768; **3**, lateral; **4**, oral; both × 3. **5, 6**, BMNH EE3788; **5**, oral; **6**, lateral; both × 3.

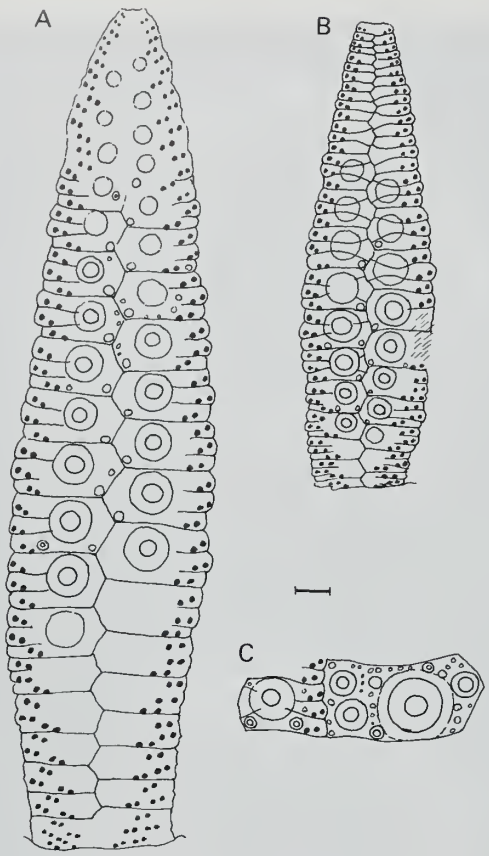


Fig. 41 Camera lucida drawings of plating in *Echinotiara perebaskinei* Lambert. **A**, BMNH EE3769, ambulacrum from apex (top) to peristome margin (bottom); **B**, BMNH EE3763, ambulacrum from apex (top) to peristome margin (bottom); **C**, ambital ambulacral and interambulacral plate, BMNH EE3763. Scale bar = 1 mm.

buccal notches are small but distinct.

The perignathic girdle structure is seen in BMNH EE3783 and EE3788. It consists of two long peg-like auricles that do not meet above the perradius. Spines and lantern are unknown.

REMARKS. This species lacks crenulate tuberculation, although preservation is usually inadequate to be certain for most specimens. It could easily be mistaken for *Orthopsis miliaris* on account of its very similar tuberculation and test shape. However, *Orthopsis* has perforate tuberculation and its ambulacral pore-pairs are strictly uniserial, not arranged in arcs of three as in *Echinotiara*. Furthermore, *Echinotiara* has well-developed phyllodes that are never seen in *Orthopsis*.

The type material described and illustrated by Lambert differs in apparently having slightly less well developed phyllodes adorally at comparable sizes, but for the present the two populations are treated as conspecific.

Cohort **IRREGULARIA** Latreille, 1825
Order **HOLECTYPOIDA** Duncan, 1889
Family **HOLECTYPIDAE** Lambert, 1899
Genus ***COENHOLECTYPUS*** Pomel, 1883

Coenholectypus inflatus (Cotteau & Gauthier, 1895)
Pl. 18, figs 7–11; Figs 42, 43A, C

1895 *Holectypus inflatus* Cotteau & Gauthier: 73, pl. 12, figs 1–4.
?1989 *Holectypus (Caenholectypus) inflatus* Cotteau & Gauthier; Ali: 401, fig. 4 (1).

TYPES. The specimen described and illustrated by Cotteau & Gauthier, from the late Cretaceous of Aftab, southern Iran.

MATERIAL STUDIED. Thirty specimens, of which 16 were used in the biometric analysis (BMNH E82644, EE3399, EE3401–04, EE3406–07, EE3409, EE3411–15, EE3417, EE3429).

OCCURRENCE. There are two morphologies found along the western foothills of the Oman Mountains:

Depressed variety: this occurs at Jebel Huwayyah, from an uncertain horizon. It is also found at Jebel Buhays (sections 1 and 2) in the lowest limestones. It is more common at Jebel Rawdah: in section 3 it occurs reasonably abundantly in bed 6 (6) and is found at a comparable level in section 4 (beds 19 and 21–22 and at top of measured section) (10). It also occurs frequently at and immediately above the level of the first major red parting in section 3 (bed 5).

More inflated, rounded forms are recorded from Jebel Huwayyah (unknown horizon); and from Jebel Rawdah, Section 2, bed 6, section 3, bed 10, section 4, bed 13.

DESCRIPTION. Tests are circular in outline and range from around 13 mm up to 56 mm in diameter. In profile their height varies from low conical to almost subglobular. Test height is 47–77% of test length (Fig. 42). The ambitus is well rounded and lies a little below midheight (Pl. 18, fig. 11).

The apical disc is small and compact with five gonopores. Genital plates are small and pentagonal and separated from one another by ocular plates that are almost as large (Fig. 43C). Madrepores occupy the entire central region.

Ambulacra are simple and uniserial, except adapically in larger specimens (40 mm diameter plus), where pore-pairs become slightly offset creating an incipient biserial arrangement. There is no pore crowding towards the peristome (Fig. 43A) and all plating is simple. Only close to the peristome does ambulacral plating become differentiated into triads with every third plate becoming enlarged. All pore-pairs are nonconjugate. There are approximately 100 pore-pairs in a column at 18 mm test length, rising to 185 at 56 mm test length (Fig. 42).

Interambulacra are standard in their structure. The periproct is oval in outline and lies close to the peristome and well separated from the ambitus (Pl. 18, fig. 7; Fig. 43A). It opens between interambulacral plates 2a,b and 6b,7a or 7a,b. Its width is 55–81% of its length (mean = 65%, SD = 7%, N = 17). The distance separating the periproct and peristome is small, only 20–50% of the periproct length; whereas the distance separating the periproct from the ambitus is much greater, being 110–260% of the periproct length (greatest in largest individuals).

The peristome is circular with feeble buccal notches. It is 15–35% of test length in diameter (mean = 23%, SD =

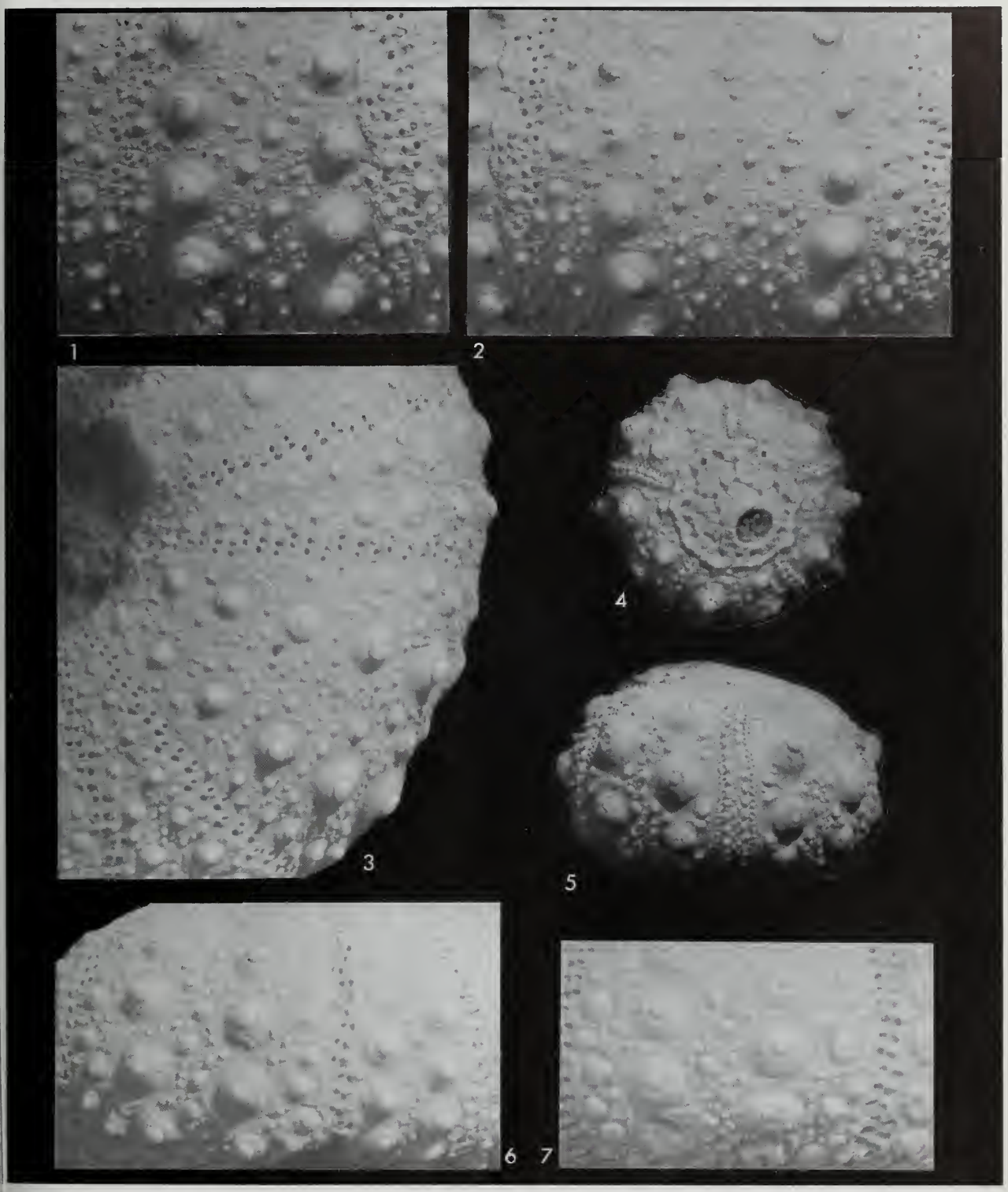


PLATE 17

Figs 1, 2 *Circopeltis? emiratus* sp. nov. BMNH EE3584, holotype, details of ambital tuberculation; **1**, ambulacrum, × 7; **2**, interambulacrum, × 5.

Figs 3, 6, 7 *Echinotiara perebaskinei* Lambert. **3, 6,** BMNH EE3774; **3**, apical, × 6; **6**, ambital detail, × 5. Jebel Rawdah, section 2, bed 4. **7,** BMNH EE3785, lateral detail, × 6. Jebel Rawdah, section 2, beds 6–8.

Figs 4, 5 *Salenia nutrix* Peron & Gauthier. **4,** BMNH EE3627, apical, × 5. Jebel Rawdah, section 1, bed 3. **5,** BMNH EE3634, lateral, × 5. Jebel Rawdah, section 2, loose in scree at level of bed 11.

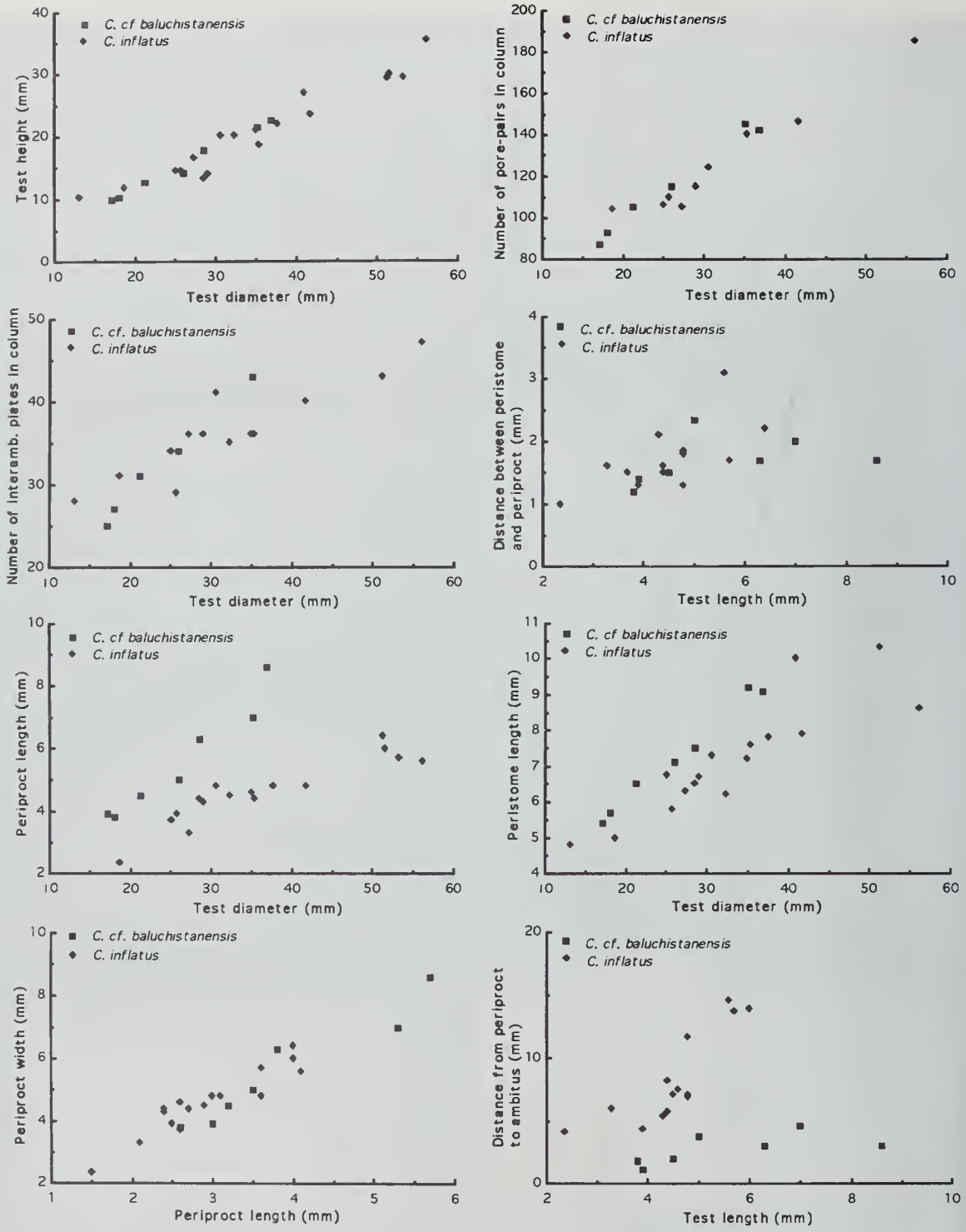


Fig. 42 Biometric data for *Coenholectypus inflatus* (Cotteau & Gauthier) and *C.* cf. *baluchistanensis* (Noetling).

4·6%, N = 16), being relatively larger in small individuals.

REMARKS. This species is easily recognised by its rounded profile, and its small periproct that lies close to the peristome and well separated from the ambitus. Although Cotteau & Gauthier's (1895) description is sketchy, it is readily recognisable from the illustrations given. Ali (1989) described two species of *Coenholectypus* from the western Oman mountains *C. inflatus* and *C. larteti* (Cotteau). Unfortunately the latter is a Cenomanian species (Smith *et al.* 1990). Because Ali gave no description and only illustrated the aboral surfaces of his

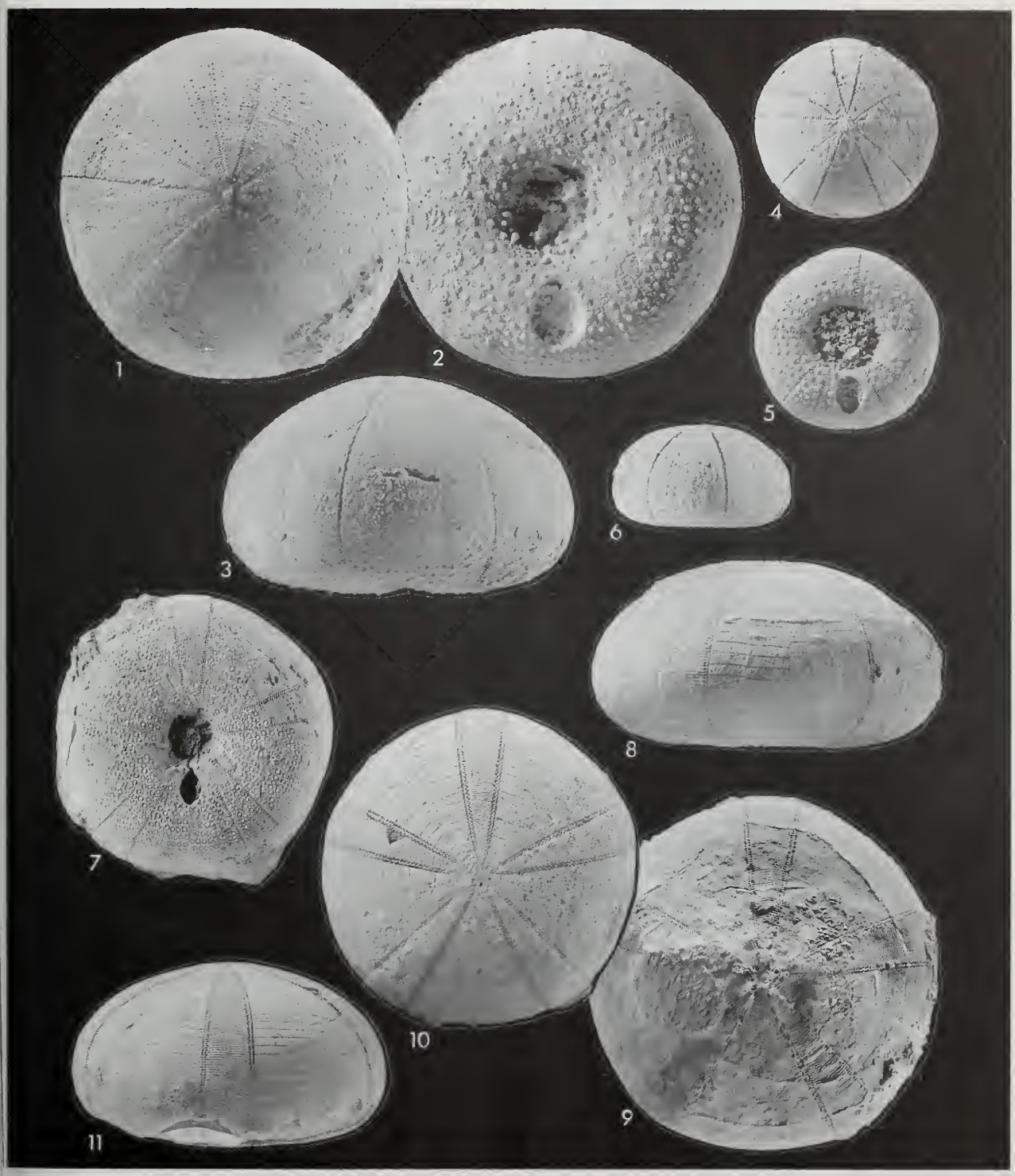


PLATE 18

Figs 1–6 *Coenholectypus* cf. *baluchistanensis* (Noetling). **1–3**, BMNH EE3389; **1**, apical; **2**, oral; **3**, lateral; all × 2. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation. **4–6**, BMNH EE 3395; **4**, apical; **5**, oral; **6**, lateral; all × 2. Jebel Rawdah, section 2, bed 11.

Figs 7–11 *Coenholectypus inflatus* Cotteau & Gauthier. **7**, BMNH EE4330; oral, × 1. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation. **8, 9**, BMNH EE3412; **8**, lateral; **9**, oral; both × 2. Jebel Buhays, section 2, lowest part of the Simsima Formation. **10, 11**, BMNH EE3424; **10**, apical; **11**, lateral; both × 1·5. Jebel Rawdah, section 3b, loose, from higher part of the section.

two forms, it is impossible to tell to which species either belongs. His assignment of one to *C. inflatus* is therefore accepted tentatively.

C. inflatus differs from *C.* cf. *baluchistanensis* (Noetling), the other species described here, on several counts. Firstly, it has finer tuberculation on its oral surface at comparable sizes. Secondly, its peristome is proportionally smaller at comparable sizes, and thirdly, its periproct is smaller and more removed from the ambitus at all sizes (Fig. 42).

There is a stratigraphical variation in profile. The taller forms, exactly comparable in form with the Iranian type, are found lower down in the sections in the coarse calcarenites: in bed 2 at Jebel Rawdah section 4, In bed 6 at section 2, and in bed 13 at section 4. The more depressed forms are found higher up in the more orbitoline-rich limestones and may represent deeper water morphological varieties.

Coenholectypus* cf. *baluchistanensis (Noetling, 1897)
Pl. 18, figs 1–6; Figs 42, 43B, D

cf. 1897 *Holectypus baluchistanensis* Noetling: 18, pl. 3, fig. 3.

MATERIAL. Thirteen specimens (BMNH EE3386–98).

OCCURRENCE. In the western Oman mountains this species was found at the following localities and horizons:
Jebel Buhays, section 1: loose in scree (3) and bed 8 (1).
Jebel Thanais, lowest 2 m of limestone section (1).
Jebel Rawdah, section 1: 20 cm below the top of bed 5 (1).
Jebel Rawdah, section 2: bed 11 (9).

It was originally described from the Maastrichtian of Baluchistan.

DESCRIPTION. Tests are circular in outline and range from 18–37 mm in diameter. They are moderately inflated in profile (Pl. 18, fig. 3), with a test height 55–62% of test length. The ambitus is rounded and lies a little below mid-height.

The apical disc has five gonopores. The four genital plates are small and pentagonal and separated from each other by ocular plates that are similar in size (Fig. 43D). The madreporite plate is large and often tumid. Madrepores are well developed over the central area.

Ambulacra are uniserial throughout, with simple nonconjugate pores. There is no hint of incipient biseriality adapically, nor any pore crowding adorally. All plates are simple, with triad development only appearing towards the peristome.

The interambulacra are standard in structure. The periproct is relatively large and opens between interambulacral plates 2a,b and 7a,b. It is oval in outline, pointed at both ends. Its width is 60–76% of its length (mean = 70%, SD = 5·7%, N = 7). It opens close to the peristome (Pl. 18, fig. 2; Fig. 43B), separated by 20–45% of the periproct length from the peristome (mean = 32%, SD = 8·4%, N = 7). It is separated from the ambitus by only a small distance in smaller individuals, some 28% of periproct length at 17 mm test length, but this increases in larger individuals to reach 65% of periproct length at a test length of 35–37 mm.

The peristome is circular in outline with deep and well marked buccal notches. It is 10–22·5% of test length in

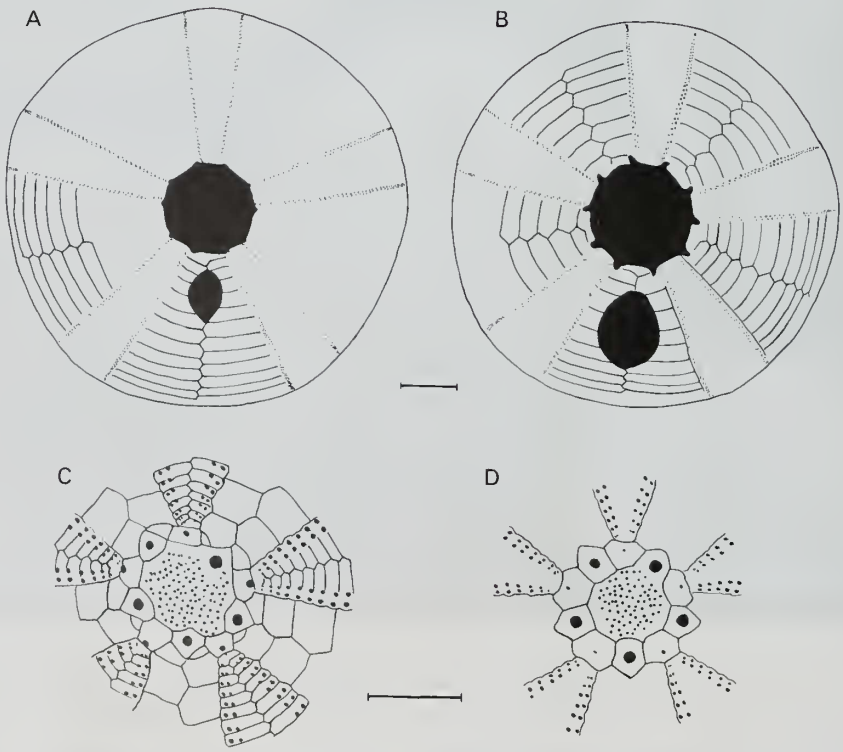


Fig. 43 Camera lucida drawings of plating in *Coenholectypus*. **A, C,** *C. inflatus* (Cotteau & Gauthier), BMNH EE3412: A, oral plating; C, apical disc. **B, D,** *C.* cf. *baluchistanensis* (Noetling), BMNH EE3389: B, oral plating; D, apical disc. Scale bars: A, B = 5 mm; C, D = 1 mm.

diameter (being relatively larger in small individuals).

REMARKS. This species is easily distinguished from the other *Coenholectypus* that occurs here, *C. inflatus*, by its larger peristome, larger periproct that extends much closer to the ambitus, and by its coarser adoral tuberculation. It also has deeper buccal notches.

C. baluchistanensis Noetling, from the Maastrichtian of Baluchistan, was established on the basis of two specimens 31 and 38 mm in diameter. Like the species described here, this has a relatively large peristome occupying much of the lower surface. Unlike the arabian specimens, the periproct of the Baluchistan species extends closer to the ambitus in the illustrated specimen. However, Noetling states that all specimens are crushed to some degree, and the illustrated specimen is damaged posteriorly. Therefore I suspect that the periproct is in reality slightly more distant from the ambitus than is actually shown. Until new material of *C. baluchistanensis* is available, the identification of Omani material as this species must remain tentative.

C. subcrassus Peron & Gauthier, from the early Maastrichtian of Algeria and Tunisia, differs from *C. baluchistanensis* in having a much larger periproct that occupies virtually the entire oral surface of the posterior interambulacrum. It is illustrated as having a broad, flat, adambital margin, unlike the arabian species. However, *C. subcrassus* and *C. baluchistanensis* are sister taxa.

Genus *COPTODISCUS* Cotteau & Gauthier, 1895

Coptodiscus magniproctus sp. nov. Pl. 19, figs 4–7; Figs 44, 45

TYPES. Holotype, BMNH EE3716, paratype, BMNH EE3715. There are no other specimens.

OCCURRENCE. Both specimens come from the base of the silty *Loftusia* beds (bed 1), at Jebel Huwayyah, section 2.

DIAGNOSIS. A *Coptodiscus* with a relatively large periproct occupying most of the oral surface of the posterior interambulacrum and opening between interambulacral plates 2 and 7. Aboral interambulacral ornament comprising a series of fine sutural pits and a set of pits along the midline of the each plate.

DESCRIPTION. Both specimens are small, but have open gonopores and are thus mature individuals. The smaller specimen is 10 mm in diameter, the larger 16 mm. Both are circular and low conical in profile, with the ambitus positioned relatively low down. Test height is about 40% of test diameter.

The apical disc is small and compact (Fig. 45A). There are five genital plates, each perforated by a gonopore. The ocular plates are almost as large as the genital plates, but are exsert and only oculars III and II abut the madreporite plate. The genital plates are contiguous around the posterior and lateral margins of the madreporite.

Ambulacra are uniserial and simple throughout, pores becoming slightly more widely spaced towards the peristome. There are three and a half ambulacral plates to an ambital interambulacral plate.

The peristome is relatively large, 25% of test diameter in diameter. It is not much invaginated. The periproct is relatively large, being 3·6 mm in length (22% of test diameter) by

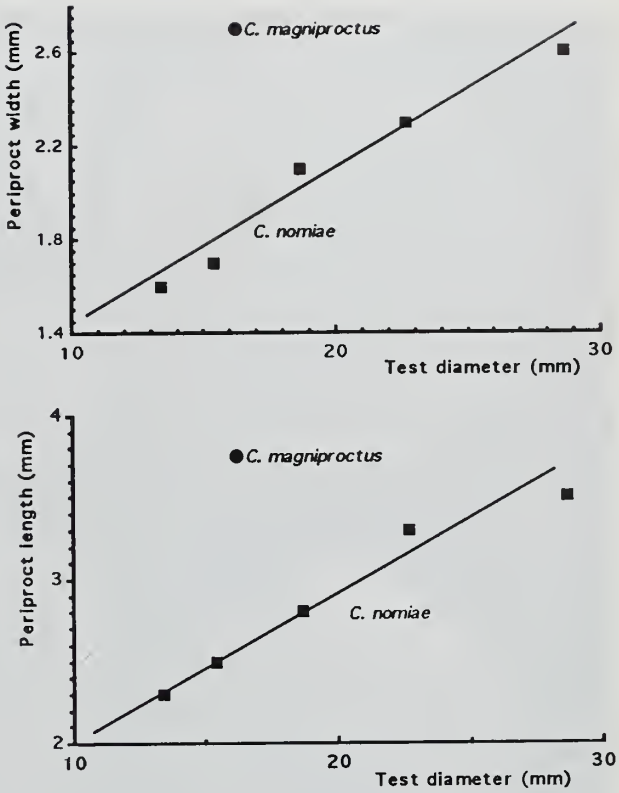


Fig. 44 Biometric data for species of *Coptodiscus*. Data from the type series of *Coptodiscus noemiae* Cotteau & Gauthier. The holotype of *C. magniproctus* sp. nov. is also plotted.

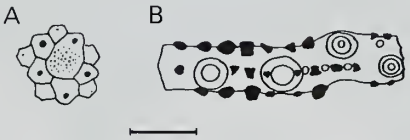


Fig. 45 Camera lucida drawings of *Coptodiscus magniproctus* sp. nov., BMNH EE3716. **A**, Apical disc; **B**, ambital interambulacral plate, adradial margin to right. Scale bar = 1 mm.

2·3 mm. It is pointed at both ends and lies close to both the peristome and the ambitus. Only 1·3 mm separates the periproct from the peristome and 1·2 mm separates the periproct from the ambitus. The periproct opens at interambulacral plate 2 and extends to interambulacral plate 7 (Fig. 44).

Tuberculation is standard with three or four primary tubercles on an ambital interambulacral plate. The surface of the test is ornamented by rows of fine pits (Pl. 19, fig. 4; Fig. 45B). These are arranged along the horizontal sutures, but are also developed along the midline of the plate in between the primary tubercles.

REMARKS. Amongst holectypoids, ornamentation of the test, as seen in this species, is found only in the genus *Coptodiscus*. Only one late Cretaceous species of *Coptodiscus* has ever been described, *C. nomiae* Cotteau & Gauthier (1895) (Pl. 19, figs 1–3; see Kier 1972 for a detailed description). *C. nomiae*, which comes from the 'Senonian' of south-

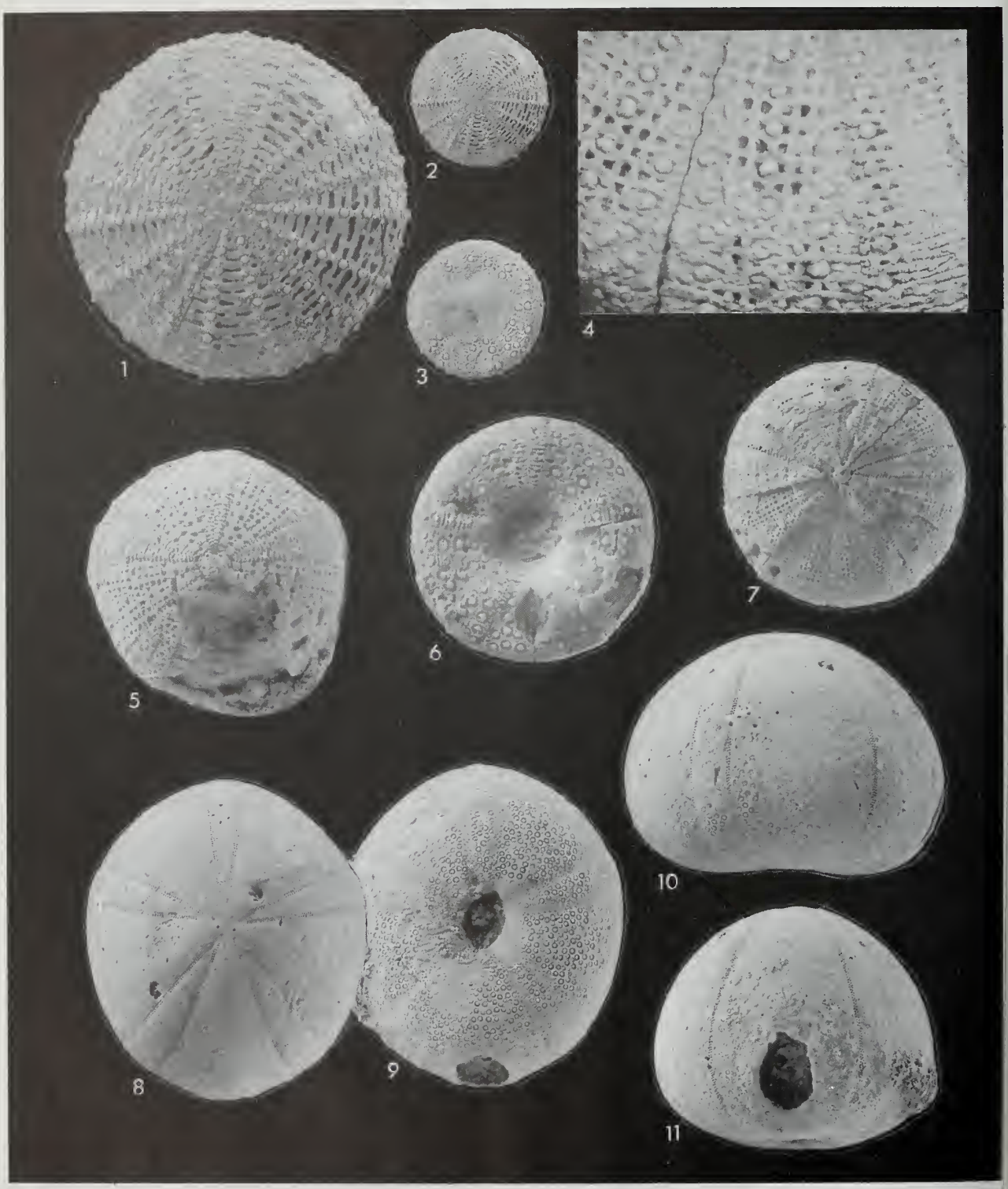


PLATE 19

Figs 1–3 *Coptodiscus noemiae* Cotteau & Gauthier. Syntype, from the Morgan Collection, Museum d'Histoire Naturelle, Paris; **1**, apical, × 5; **2**, apical, × 2; **3**, oral, × 2; Senonian, Khianan, Iran.

Figs 4–7 *Coptodiscus magniproctus* sp. nov. Jebel Huwayyah, section 2, bed I. **4, 6, 7,** BMNH EE3716, holotype; **4**, detail of adapical ornamentation, × 10; **6**, oral, × 3; **7**, apical, × 3. **5**, BMNH EE3715, paratype, apical surface, × 5.

Figs 8–11 *Conulus douvillei* Cotteau & Gauthier. BMNH EE4306; **8**, apical; **9**, oral; **10**, lateral; **11**, posterior; all × 2. Jebel Thanais, lowest 2 m of the Simsima Formation.

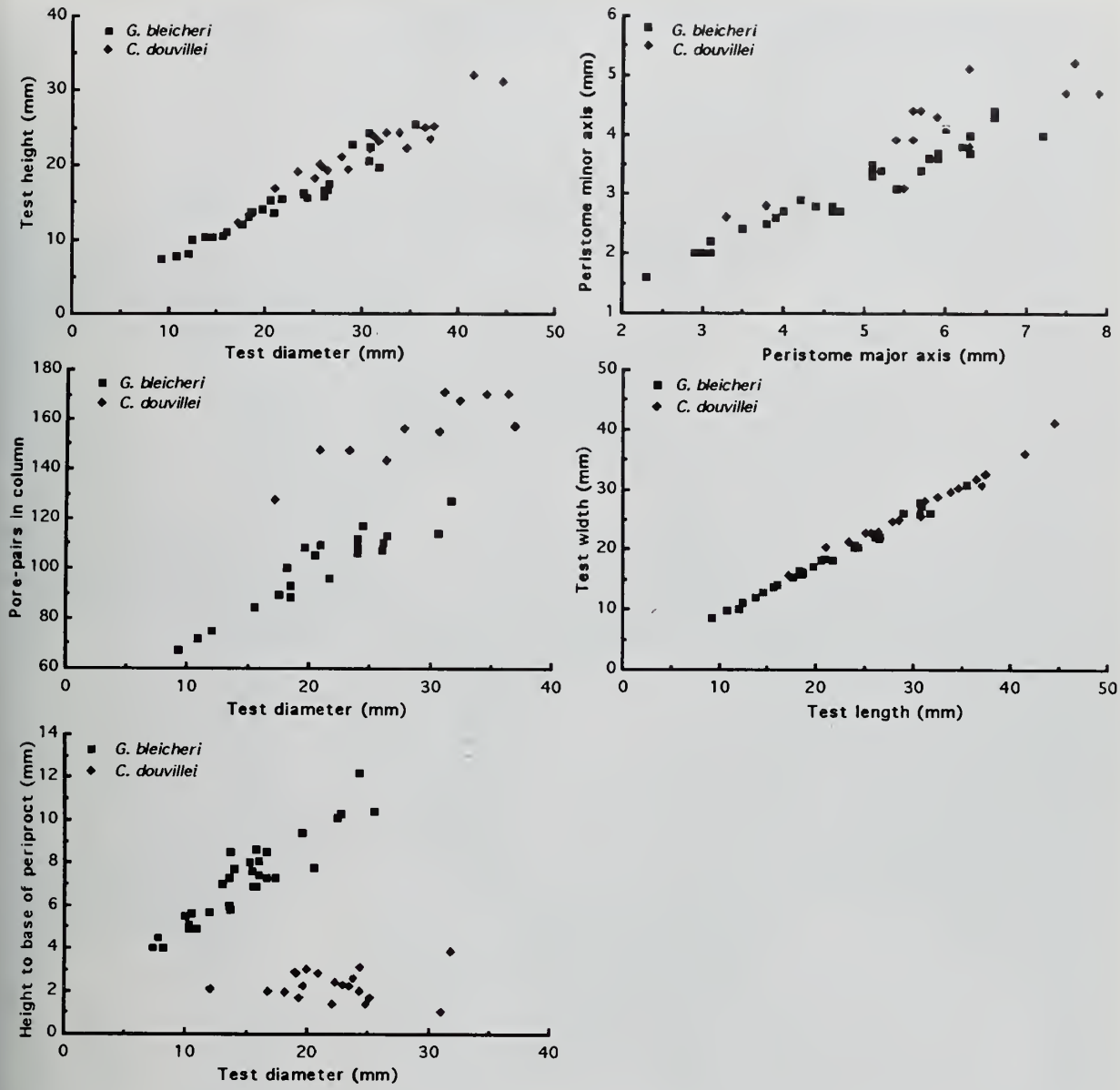


Fig. 46 Biometric data for '*Globator*' *bleicheri* (Thomas & Gauthier) and *Conulus douvillei* (Cotteau & Gauthier).

ern Iran and the late Campanian of Saudi Arabia and Oman, differs from our species in several important details. Firstly, its periproct is very much smaller at comparable sizes (Fig. 44) and it lies well separated from the peristome, with at least three and usually four interambulacral plates in each column separating the two openings, as opposed to the two in *C. magniproctus*. The periproct is also considerably more rounded in *C. nomiae*. A second immediately apparent difference is in the style of ornamentation developed aborally. In *C. nomiae* there is a single laterally extensive sutural pit on either side of the primary tubercle, also, intraplate pits are not as well developed, whereas in *C. magniprocta* there is a well-developed row of sutural pits (compare Pl. 19, figs 1, 4).

Family **CONULIDAE** Lambert, 1911
Genus ***'GLOBATOR'*** Agassiz, 1840

REMARKS. The genus *Globator* was erected by Agassiz (1840) for small, ovoid conulids with large periprocts opening above the ambitus. The type species is *Globator nucleus* Agassiz, but this is based on a juvenile *Conulus rotundus* Goldfuss and thus *Globator* falls into synonymy with *Conulus*. However, there is a distinct clade of ovoid conulids with large, supra-ambital periprocts that can be recognized. This group is currently under revision (Smith & Wright, in prep.) and for the moment we retain its members under the name '*Globator*'.

'Globator' bleicheri (Gauthier, 1889) Pl. 20, figs 1–10; Figs 46, 47A, B, F–I, 48A

1889 *Pyrina bleicheri* Gauthier: 51, pl. 3, figs 15–18.
1895 *Pyrina orientalis* Cotteau & Gauthier: 68, pl. 11, figs 1–8.
1897 *Pyrina zumoffeni* de Loriol: 158, pl. 7, fig. 1.
1967 *Pyrina ovulum* Agassiz; Devries: 177, pl. 5, figs 19–21.
1987 *Pseudopyrina bleicheri* (Thomas & Gauthier); Zhagbib-Turki: 167.
1989 *Globator orientalis* (Cotteau & Gauthier); Ali: 403, fig. 5 (4–5).

MATERIAL STUDIED. This is a common species in the lower beds of the Simsima Formation and a large number of specimens were available for study. There are 208 specimens in the collections made. Of these the following were measured: BMNH EE4107, EE4116–19, EE4121, EE4129, EE4130, EE4132–34, EE4139–41, EE4144–45, EE4154–57, EE4163, EE4172, EE4174, EE4186, EE4208, EE4217, EE4232, EE4249, EE4251, EE4253–54, EE4257.

OCCURRENCE. The species was first described from the late Cretaceous (late Campanian) of Jebel Atra, Tunisia. It has also been described from the Upper Senonian of Derre-i-Chahr and Endjir-kouh, southern Iran (Cotteau & Gauthier 1895) and the late Cretaceous of Palestine (de Loriol 1897) and Turkey (Devries 1967). In the western margins of the central Oman Mountains this species is found at the following localities and levels:
Jebel Buhays, section 1: loose in scree (96).
Jebel Buhays, section 2: loose in scree (3).
Jebel Buhays, section 3: lowest 2 metres (1).
Jebel Thanais: lowest couple of metres of section (5).
Jebel Aqabah: basal shell bed (2).
Jebel Faiyah, section 1: arbaciid level *ca.* 4 m above base (12).
Jebel Huwayyah, section 1: beds 14 and 15 (54).
Jebel Rawdah, section 1: bed 6 (1); top of bed 4 (15); bed 3 (49); loose (2).
Jebel Rawdah, section 2: bed 6 (1); bed 11 (10); bed 13 (1); bed 14 (7); bed 16 (3); bed 19 (8); bed 20 (1); bed 21 (1) loose in scree just above bed 12 (2); loose in scree, mostly near base (14).
Jebel Rawdah, section 3: bed 1 (11); bed 5 (9); bed 9 (1); bed 11 (1); loose in scree (3).
Jebel Rawdah, section 4: bed 2 (9); bed 4 (4); bed 5 (1); bed 8 (3); bed 10 (10); bed 14 (3); bed 20 (1).

DIAGNOSIS. An oval, rather depressed '*Globator*' with a large, strongly ellipsoidal peristome. The periproct lies high on the posterior surface and is visible from above but not from below. Pore-pairs in weak arcs only towards the peristome, not forming multiple rows. Genital plates 3 and 4 separated by ocular plate IV in adults.

DESCRIPTION. Tests range from 9 to 35 mm in length and are oval in outline and profile. Test width is 82–91% of test length (mean = 86%, SD = 2·6%, N = 32; Fig. 46) with the widest point on the test coincidental with the posterior portion of the anterior ambulacra. Test height is 61–80% of test length (mean = 70%, SD = 5·3%, N = 32) and the tallest point on the test is subcentral. Tests in profile have a relatively broad, flat apex and base and a rounded ambitus (Pl. 20, figs 3, 8).

The apical disc is more or less central and is tetrabasal (Fig. 47F–H). Genital plate 2 is considerably larger than the other four genital plates and is covered in madrepores. Genital plate 3 is the smallest and in the great majority of specimens is separated from genital plate 4 by ocular plate 4, which abuts genital plate 2. Genital plates 3 and 4 are found in contact only in small individuals. The posterior pair of genital plates are in contact posterior to genital plate 2. Ocular plates are pentagonal in outline and project.

Ambulacra are uniserial and pore-pairs are undifferentiated. Above the ambitus they are very strictly uniserial (Fig.

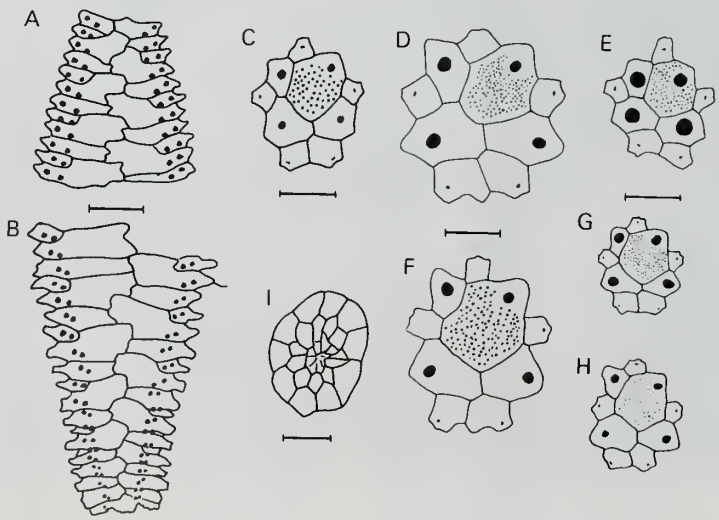


Fig. 47 Camera lucida drawings of plating in '*Globator*' and *Conulus*. **A, B, F-I**, '*G.*' *bleicheri* (Thomas & Gauthier). A, B, BMNH EE4187; A, adapical ambulacral plating; B, adoral ambulacral plating, peristomial margin at base; F, BMNH EE4186, apical disc; G, BMNH EE4148, apical disc; H, BMNH EE4154, apical disc; I BMNH EE4151, peristomial plating. **C-E**, *Conulus douvillei* (Cotteau & Gauthier), apical disc plating: C, BMNH EE4204; D, BMNH EE4277; E, BMNH EE4211. Scale bars = 1 mm.

LATE 20

igs **1–10** *'Globator' bleicheri* (Peron & Gauthier). **1–4**, Topotype specimen of *Pyrina orientalis* Cotteau & Gauthier, from the Morgan Collection, Museum d'Histoire Naturelle, Paris; **1**, oral; **2**, apical; **3**, lateral; **4**, posterior; all × 2. Senonian, Poucht-e-Kouk, Iran. **5, 6, 10**, BMNH EE4251; **5**, apical; **6**, oral; **10**, posterior; all × 2. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation. **7–9**, BMNH EE4208; **7**, posterior; **8**, lateral; **9**, apical; all × 2. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation.

igs **11–16** *Conulus douvillei* (Cotteau & Gauthier). **11, 12**, topotype specimen from the Morgan collection, Museum d'Histoire Naturelle, Paris; **11**, oral; **12**, lateral; both × 2. Senonian, Khianan, Iran. **13–16**, BMNH EE4308; **13**, oral; **14**, apical; **15**, posterior; **16**, lateral; all × 2. Jebel Thanais, lowest 2 m of the Simsima Formation.

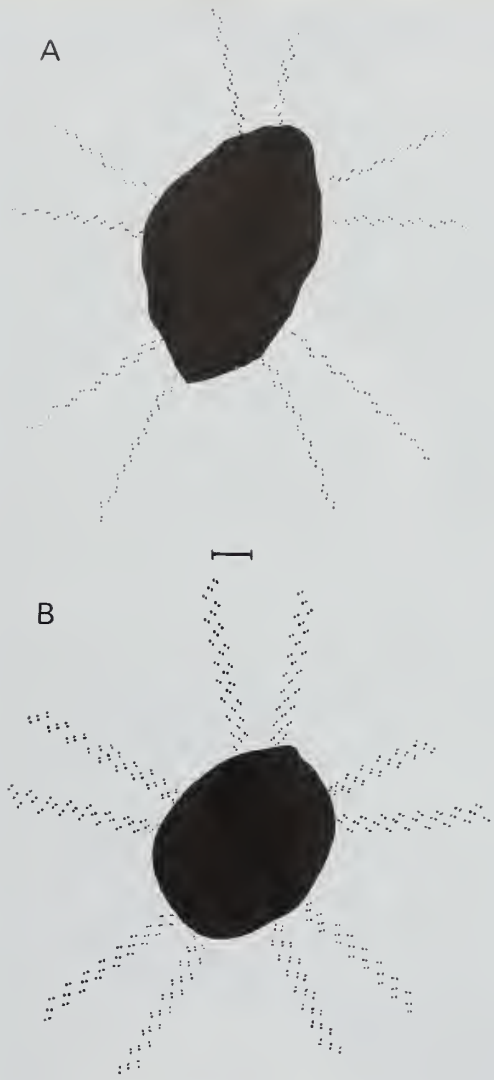


Fig. 48 Camera lucida drawings of adoral pore arrangement. **A**, *'Globator' bleicheri* (Thomas & Gauthier), BMNH EE4187; **B**, *Conulus douvillei* (Cotteau & Gauthier), BMNH EE4309. Scale bar = 1 mm.

47A), but towards the peristome they become weakly arcuate and reduce in pore-diameter size (Figs 47B, 48A). There are about 88 pore-pairs in a column at 18 mm test length, rising to 127 at 32 mm test length (Fig. 46). Plates are compound in the pyrinoid style, with a single small demiplate in each triad (Figs 47A, B). All plate sutures are denticulate.

The periproct is large and tear-drop shaped, pointed adapically (Pl. 20, figs 7, 10). It lies on the posterior surface relatively high on the test, so that it is visible when viewed from above, but not from below. Periproct height is 28–46% of the test height (mean = 36%, SD = 4·6%, N = 29) and periproct width is 56–80% of its height (mean = 65%, SD = 5·8%, N = 27). The distance from the base of the periproct to the base of the test is 38–62% of the test height (mean = 49%, SD = 5·6%, N = 31).

The peristome is oblique and broadly fusiform in outline, with the long axis running from interambulacrum 3 to ambulacrum I (Pl. 20, fig. 6). There is hardly any invaginated lip developed around the peristome, although the oral surface does curve inwards towards the periproct slightly.

Tuberculation is uniform throughout, with semi-regular and slightly sunken primary tubercles scattered over the surface, surrounded by a very dense miliary granulation. There is no internal butressing.

REMARKS. This species is easily distinguished from the other species of Conulidae, *Conulus douvillei,* that occurs here. *C. douvillei* has a periproctal opening that lies close to the base of the test, whereas the periproct in *'G.' bleicheri* lies high on the posterior and is separated by a considerable distance from the base. This is not a size-related character since there is clear separation of the two species at all sizes (Fig. 46). A second difference concerns the development of phyllodes adorally. In *'G.' bleicheri* the pore-pairs become slightly arcuate adorally (Fig. 48A), but even in the largest specimens they never become triserially arranged. Adoral pore-pairs in *C. douvillei*, by contrast, are arranged triserially across much of the oral surface (Fig. 48B). Finally, in the apical disc plating of *'G.' bleicheri* genital plate 2 almost always reaches to ocular IV separating genital plates 3 and 4. In *C. douvillei* genital plate 2 does not reach ocular plate IV and genital plates 3 and 4 maintain firm contact.

This species has previously been recorded from the Oman mountain region by Ali (1989) and Smith (in Skelton *et al.* 1990) under the name *Globator orientalis* (Cotteau & Gauthier). *'G.' orientalis* (Pl. 20, figs 1–4) was described from the late Cretaceous of southern Iran by Cotteau & Gauthier (1895). However, it appears virtually indistinguishable in form to *'Globator' bleicheri* Thomas & Gauthier, from the late Campanian of Tunisia (Zhagbib-Turki 1987). The only slight difference between these two forms is that *'G.' orientalis* may have a slightly smaller peristome. For the present, however, the two species are synonymized.

Genus *CONULUS* Leske, 1778

Conulus douvillei (Cotteau & Gauthier, 1895) Pl. 19, figs 8–11; Pl. 20, figs 11–16; Figs 46, 47C–E, 48B

1895 *Echinoconus douvillei* Cotteau & Gauthier: 70, pl. 11, figs 9–13.
1932 *Pyrina mortenseni* Checchia-Rispoli: 21, pl. 2, figs 1–3, pl. 3, figs 1, 2.
?1967 *Conulus douvillei* (Cotteau & Gauthier); Devries: 184, pl. 5, figs 22–25.
1972 *Globator mortenseni* (Checchia-Rispoli); Kier: 70, figs 35, 36, pl. 44, figs 1–7.
1989 *Globator mortenseni* (Checchia-Rispoli); Ali: 403, Fig. 4 (6–7).

TYPES. The syntypes are the five specimens whose dimensions are cited by Cotteau & Gauthier (1895: 70). They may be represented amongst material in either the Cotteau Collection (Lyon) or the Morgan Collection (Museum d'Histoire Naturelle, Paris), but none have been definitely identified.

MATERIAL STUDIED. This species is less common than *'Globator' bleicheri*, but is never the less well represented in the collections. There are 39 specimens, of which the following were measured: BMNH EE4211, EE4250, EE4277, EE4279–80, EE4283, EE4285, EE4287, EE4291, EE4898–99, EE4301, EE4304–06, EE4308, EE4310.

OCCURRENCE. This species is found in the western Oman Mountains at the following levels:
Jebel Huwayyah, section 1: beds 3–5 (1).
Jebel Buhays, section 1: loose, derived from lowest few metres of section (19).
Jebel Thanais: lowest few metres of the Simsima Formation (11).
Jebel Rawdah, section 2: bed 14 (1); bed 15 (2); bed 21 (3); loose, mid-section (1).
Jebel Rawdah, section 3: loose (4).
Jebel Rawdah, section 4: beds 8/9 (1); bed 13 (1); loose in scree (1).

Outside Oman, the species is known from Libya, Saudi Arabia, southern Iran and Assam, India.

DIAGNOSIS. A species of *Conulus* with a rounded to strongly fusiform peristome which is not sunken. Periproct situated relatively low on the posterior surface, not visible from above. Pore-pairs adorally arranged triserially. Apical disc with genital plates 3 and 4 always in contact. Test profile subconical.

DESCRIPTION. Tests range from 17 to 45 mm in length and are ovoid to rounded pentagonal in outline. Test width is 82–96% of test length (mean = 88%, SD = 3·2%, N = 18) and the widest point coincides with the posterior part of the antero-lateral ambulacra. Test height is 64–81% of test length (mean = 72%, SD = 4·9%, N = 20) and in profile the test has a broad, flat base and is rounded subconical above (Pl. 20, figs 11–16).

The apical disc lies centrally and is tetrabasal. Genital plate 2 abuts the other three genital plates but never reaches ocular plate 4 to separate genital plates 3 and 4 (Figs 47C–E). Genital plates 4 and 1 are always in contact behind the madreporite. There appears to be some degree of differentiation in gonopore size, suggestive of sexual dimorphism.

Ambulacra are straight and compound in the pyrinoid style. Above the ambitus pore-pairs are strictly uniserial, but below the ambitus they become offset into three discrete columns and these continue to the peristome edge (Pl. 19, fig. 9; Pl. 20, fig. 11; Fig. 48B).

The periproct lies on the posterior border, close to the base (Pl. 20, fig. 15). It is tear-drop shaped, being pointed adapically. Its height is 28–40% of the test height (mean = 35%, SD = 3·2%, N = 20) and its width is 55–77% of its height (mean = 65%, SD = 6·2%, N = 19). The base of the periproct lies 3–17% of the test height above the base (mean = 11%, SD = 3·6%, N = 20). The periproct is just visible from beneath, but is not seen from above (Pl. 19, figs 8, 9).

The peristome is oval to fusiform in outline and is not invaginated, although the oral surface may be slightly depressed towards the peristome. Its length is 14–23% of the test length (mean = 20%, SD = 2·7%, N = 13). Its width is 56–81% of its length (mean = 70%, SD = 8·1%, N = 13). It is oblique, with its long axis orientated from interambulacrum 3 to ambulacrum I (Pl. 19, fig. 9).

REMARKS. The distinction between this species and '*Globator*' *bleicheri* is detailed above. This species comes closest to *Conulus giganteus* Noetling (*C. gigas* Cotteau, *C. ataxaensis* Cotteau) but in this species complex the peristome is less ovoid and is distinctly more invaginated than *C. gigas* at least. Whether the Middle Eastern species turn out to be sufficiently distinct remains to be seen.

Order **CASSIDULOIDA** Claus, 1880
Family **CLYPEOLAMPADIDAE** Kier, 1962

DIAGNOSIS (following Kier, 1962). Cassiduloids with a domed test and flat base. Petals long and straight, apical disc tetrabasal, periproct inframarginal and transverse, bourrelets with three or more columns of pores and with buccal pores present.

TYPE GENUS. *Clypeolampas*, type species *C. ovatus* Lamarck, 1816.

OTHER GENERA INCLUDED. *Hungaresia* Szorenyi, type species *Hungaresia hungarica* Szorenyi (junior synonym of *Clypeolampas ovum* Grateloup); *Vologesia* Cotteau & Gauthier, type species *V. tataosi* Cotteau & Gauthier.

REMARKS. Lambert (1919) claimed that the original figure and description of *Clypeolampas ovatus* Lamarck (1816: 22) was inadequate for certain identification, and thus used the name *Clypeolampas leskei* Goldfuss (1829) as the oldest available name. However, Kier (1962: 190) accepted *C. ovatus* Lamarck as a valid designation and sunk *C. leskei* Goldfuss in synonymy.

There are eighteen nominal species assigned to the three genera listed above. The differentiation of the three genera is, however, unclear. *Vologesia* was established by Cotteau & Gauthier (1895: 65) for a late Cretaceous species from Aftab, Iran, *V. tataosi* Cotteau & Gauthier. This is based on a single small individual, subcircular in plan view, with poorly developed bourrelets and the peristome positioned close to the anterior border. No other species were included in this genus until Lambert (1919) revised the then known members of *Clypeolampas*. He separated species into two groups; those with uniform aboral tuberculation, all tubercles being scrobiculate, and those forms which had a second kind of aboral tuberculation composed of nonscrobiculate pustules. The former he assigned to *Vologesia*, the latter to *Clypeolampas*. Lambert (1919) placed the following species in *Vologesia*: *C. ovum* Grateloup, *C. acuta* Desmoulins, *C. conica* Arnaud, *C. toucasi* Lambert, *C. gossauviensis* Lambert and a small undescribed Maastrichtian form. In *Clypeolampas* Lambert placed *C. leskei* Goldfuss [=*C. ovatus* Lamarck], *C. perovalis*, Arnaud, *C. orbicularis* Arnaud, *C. lestelei* Cotteau, *C. vishnu*, Noetling, *C. douvillei* Lambert and *C. mengaudi* Lambert.

In 1955, Szorenyi erected the genus *Hungaresia* for the new Santonian species *H. hungarica* Szorenyi of Hungary. This species appears to be identical in many important respects to the common Santonian species *Clypeolampas ovum* Grateloup, and Kier (1962: 191) synonymized the two genera, making *Hungaresia* a junior synonym of *Vologesia*.

Kier (1962, 1966) followed Lambert's generic differentiation, distinguishing *Clypeolampas* from *Vologesia* by its nonscrobiculate pustules developed adapically, and by its better developed floscelle. However, Kier's concept of *Vologesia* was based not on the type species but on *Clypeolampas ovum* Grateloup and is thus misleading.

There are very few stable characters on which to subdivide the group, the following being amongst the most informative.

(1) Aboral pustules developed. In some species there are characteristic pustules over the adapical surface that are slightly larger than the normal tuberculation and give the surface a rugose appearance. These are not tubercles for spine articulation, as they have no articular surface or sur-

rounding scrobicule. Instead they resemble the pustular calcite formed in species of *Conulus* or *Echinoneus* (Smith 1980). Their function is unknown but it may be to do with deterring parasitic and commensal settlement. Pustules are developed in a number of species, including the type *C. ovatus* Lamarck.

(2) The position of the peristome seems highly stable and distinctive. In *Vologesia tataosi* and *V. rawdahensis* the peristome lies close to the anterior border, with the anterior edge lying between 20 and 25% of the test length from the anterior. In almost all other species the peristome is subcentral, lying between 30 and 40% of the test length from the anterior. Only one species, *Clypeolampas toucasi* Lambert is intermediate in this respect, with its peristome between 25 and 30% of test length from the anterior.

(3) Elongation of the peristome. Only *Vologesia rawdahensis* Ali has such a laterally elongate peristome. In other species the peristome is suboval.

(4) The degree to which the floscelle projects as prongs over the peristome is to some extent size dependent, with more prominent floscelles in larger individuals. However, at a similar size it is apparent that *Vologesia tataosi*, *V. rawdahensis* and *Clypeolampas toucasi* show virtually no floscelle development, whereas *C. ovatus* and its synonyms and *C. perovalis* have very pronounced floscelle projection. In *C. lestelei*, *C. ovum*, and *C. conicus* as well as probably *C. helios*, the floscelle is slightly swollen but not projecting.

(5) The periproct is usually unambiguously positioned on the flat oral surface, but in a few species such as *C. helios* and *C. ovum*, the periproct lies subambitally because of the strongly inflated test profile.

(6) The apical disc is definitely tetrabasal in *C. lestelei*, *C. ovum* and *Vologesia rawdahensis*, but monobasal in *C. ovatus*.

(7) The arrangement of pores in the bourrelets, though to some extent size dependent, offers some differentiation. In *C. ovatus* there are many pores irregularly scattered between inner and outer columns in each half ambulacrum. By contrast *C, ovum* and *Hungaresia hungarica* have only the inner and outer series of pores. If *C. conicus* is just a variety of *C. ovum* as is suspected, then some specimens may have a few pores forming a mid row. The same is true of *Vologesia rawdahensis* where individuals have either two or three rows.

From this the following supraspecific taxonomy is proposed:

Clypeolampas Lamarck: Large forms with moderate to well developed bourrelets, subcentral peristome and aboral calcite pustules. Species included; *C. ovatus* Lamarck (includes *C. leskei* Goldfuss, *C. mengaudi* Lambert, *C. douvillei* Lambert, *C. orbicularis* Arnaud), Upper Campanian-Maastrichtian of Spain, southern France, Turkey; *C. perovalis* Arnaud, Lower and Middle Campanian of Gironde, France; ?*C. lestelei* Cotteau, ?Danian of Saint Cirac, Ariège, France.

Vologesia Cotteau and Gauthier. Distinguished from *Clypeolampas* by its anterior peristome without floscelle development. Type species *V. tataosi* Cotteau & Gauthier, Upper Senonian of Louristan, Iran; *V. rawdahensis* Ali, Maastrichtian of the Oman Mountains; *V. toucasi* (Lambert), Campanian of the Pyrenees, France.

Hungaresia Szorenyi. Smaller, ovoid forms with subcentral, pentagonal peristome with swollen but not projecting floscelles, no aboral pustules and subambital rather than fully adoral periproct. Type species, *H. ovum* (Grateloup) [includes *H. hungarica* Szorenyi], Upper Santonian of France, Pyrenees, Hungary. Other species included: *H. helios* (Noetling), ?Maastrichtian, Mari Hills, Baluchistan.

Unplaced taxa: *Clypeolampas conicus* Arnaud (U. Santonian to L. Campanian, SW France) and *C. acuta* Desmoulins (pores in bourrelets shown as forming two columns only). material of these species has not been seen and so they cannot be placed with any confidence from the published descriptions and figures.

C. vishnu Noetling: based on a single worn specimen, inadequately known *nomen dubium*.

C. gossaviensis Lambert: based on a single, poorly preserved specimen and indeterminate from description and figure *nomen dubium*.

Genus ***VOLOGESIA*** Cotteau & Gauthier, 1895

TYPE SPECIES. *Vologesia tataosi* Cotteau & Gauthier, 1895, by original designation.

OCCURRENCE. Late Cretaceous ('Upper Senonian') of Iran; Maastrichtian of the United Arab Emirates and Oman.

DIAGNOSIS. Clypeolampadids with an anteriorly positioned peristome lying 20–30% from the anterior border. Peristome wide, pentagonal with bourrelets hardly developed. Phyllodes with two or three rows of pores in each half ambulacrum. Apical disc tetrabasal.

REMARKS. *Vologesia* is distinguished from *Clypeolampas* by its lack of aboral pustules and its poorly developed floscelles and bourrelets. It is distinguished from *Hungaresia* by its lack of floscelles, its more transverse peristome and its more anterior peristome.

Vologesia rawdahensis Ali, 1989 Pl. 21, figs 1–5; Figs 49–51

1989 *Vologesia rawdahensis* Ali: 406, fig. 5 (13).

TYPES. Three specimens in the Geology Museum, United Arab Emirates University, Al Ain, United Arab Emirates.

MATERIAL STUDIED. Seven specimens, of which five (BMNH EE3383–85, EE4326, EE4329) are well enough preserved to be included in the biometric analysis.

OCCURRENCE. This species is known only from the Simsima Formation of the western margins of the Oman Mountains. Specimens were found at the following localities and horizons:

Jebel Buhays, section 1: loose in the scree, derived from the lowest few metres of Simsima Formation (5).

Jebel Buhays, section 2: loose in the scree, derived from the lowest 2 m of Simsima Formation (1).

Jebel Thanais: lowest 2 m of Simsima Formation (1).

Jebel Rawdah, section 2: bed 19 (1).

Jebel Rawdah, section 3: bed 8 (1).

DESCRIPTION. Tests are flat-based and rounded to subconical in profile (Pl. 21, figs 1–4), with a relatively sharp ambitus situated low down. In outline the test is ovoid with a rounded anterior and a distinctly more pointed posterior. Tests range in length from 46 to 68 mm. Test width is 75–77% of test length and test height 53–62% of test length (Fig. 49). The tallest part of the test is central or slightly anterior of centre.

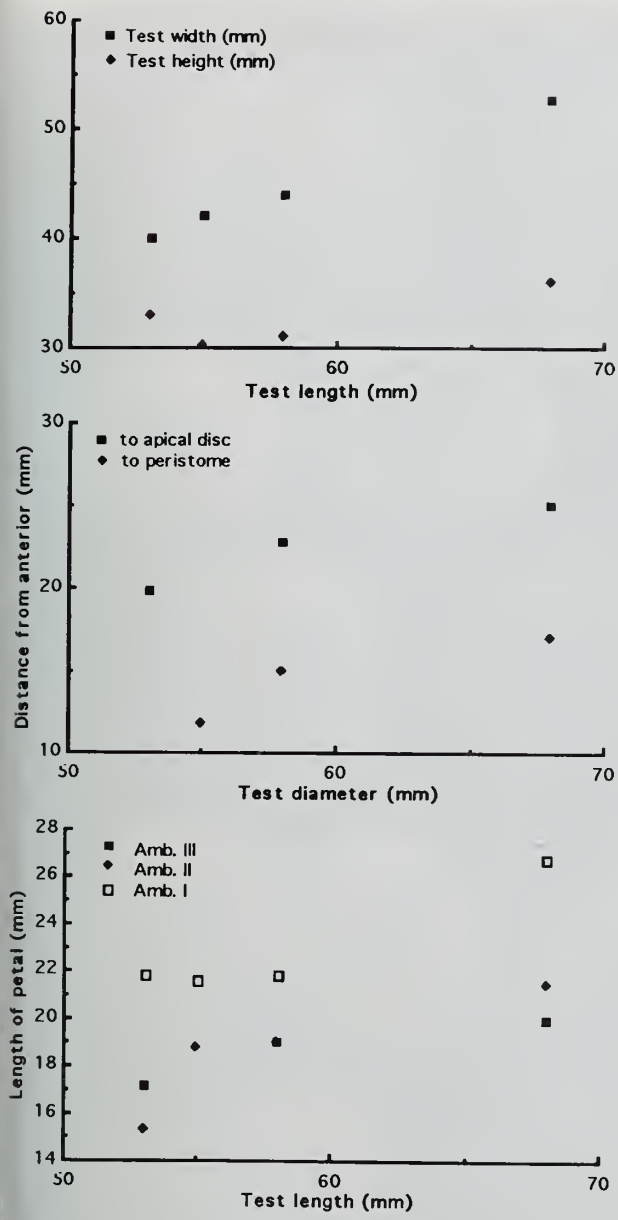


Fig. 49 Biometric data for *Vologesia rawdahensis* Ali.

The apical disc is tetrabasal (Fig. 51B), with the madreporite very large and occupying the centre. Other genital plates are much smaller and pushed far out into the adjacent interambulacra. The apical disc lies 37–39% of test length from the anterior border (Fig. 49).

Petals are relatively long and straight or only very slightly bowed. They are open distally and extend most of the distance towards the ambitus. The posterior petals are always slightly longer than the anterior three petals. They are composed of an inner circular pore and a highly elongate outer slit-like pore, joined by a furrow. There are 51 pores in a petal column in a 53 mm individual and 57 in a 68 mm individual. Pores below the petal are all single.

The peristome is pentagonal in outline and very much wider than long (width is 1·7–2·0 times greater than length). It is straight sided and only slightly invaginated (Pl. 21, fig. 5; Fig. 50) and bourrelets are hardly developed. It lies 21–27% of the test length from the anterior border. Phyllodes are relatively short and are not depressed in the slightest. In some individuals there are only two columns of pores in each half ambulacrum, whereas in others there are three columns. The outer series is composed of about 12 pores, the inner series of 7 or 8 pores and the mid series, where present, of 4 or 5 pores (Fig. 51). The inner and middle series of pores are borne on occluded plates. Buccal pores are present.

The periproct lies on the oral surface at the posterior. It is oval in outline, approximately twice as wide as long and approximately the same size as the peristome.

Aboral tuberculation is fine and uniform, oral tuberculation slightly coarser and becoming less dense towards the midline. There is a broad tubercle-free band down the midline in the posterior interambulacrum running between the peristome and periproct. This is lightly pitted (Pl. 21, fig. 5).

REMARKS. This species was erected by Ali (1989) on the basis of three specimens from Jebel Rawdah, Oman. It differs from *V. tataosi* Cotteau & Gauthier, from a similar horizon in southern Iran, by being more elongate and pointed posteriorly, and by having a smaller, more transversely elongate mouth (if the original figures of this species are true to life). The Iran species was, however, based on a single individual 27 mm in test length, and there is the possibility that with more material the two species may eventually prove to be synonymous.

Family **FAUJASIIDAE** Lambert, 1905
Genus ***FAUJASIA*** d'Orbigny, 1856

TYPE SPECIES. *Pygurus apicalis* Desor, by subsequent designation of Lambert & Thièry, 1921: 273.

OTHER SPECIES INCLUDED. Only one other species, *Faujasia eccentripora* Lees. Two species previously ascribed to *Faujasia* were transfered to other genera by Kier (1962): *F. faujasi* (Desmoulins) to *Eurypetalum* and *F. chelonium* Cooke to *Domechinus*.

DIAGNOSIS. Small ovoid cassiduloids with a monobasal apical disc in which the genital pores open through interambulacral plates. Petals broad, closed distally and strongly petaloid in form. Periproct small, circular and inframarginal. Peristome small, anterior with short, arcuate phyllodes in two columns and with buccal pores, and strongly projecting bourrelets.

OCCURRENCE. Maastrichtian of Belgium, France, Oman and the United Arab Emirates.

REMARKS. Kier (1962: 137), in discussing this genus, was uncertain whether *F. eccentripora* Lees truly belonged here, since its apical disc plating had never been described. As shown below, this species has an identical arrangement of gonopores opening within the adapical portion of the interambulacra as characterizes *F. apicalis* Desor and thus is clearly closely related. The derived position of gonopores outside apical disc plating distinguishes these two species from all other cassiduloids.

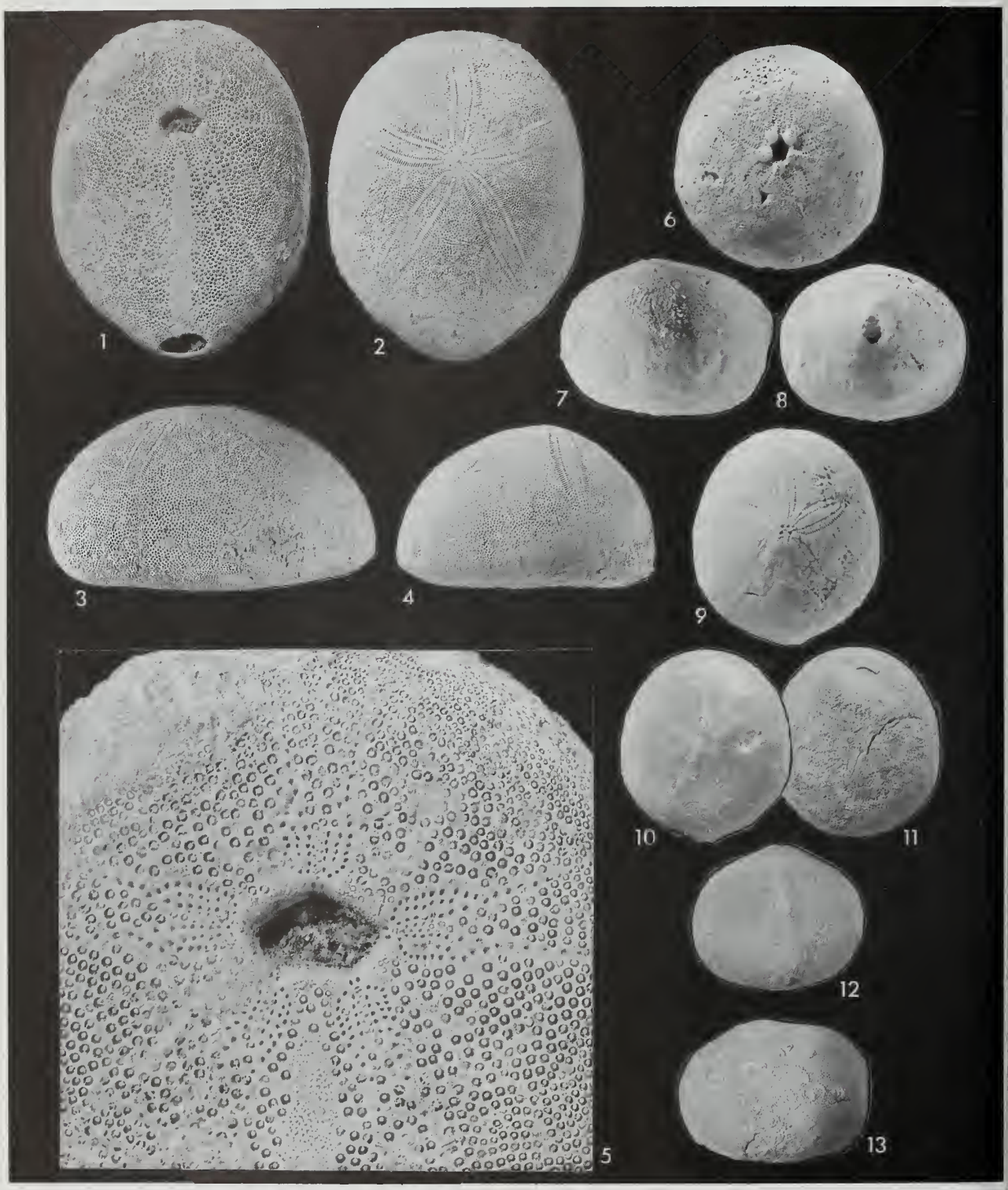


PLATE 21

Figs 1–5 *Vologesia rawdahensis* Ali. **1–3, 5,** BMNH EE4326; **1**, oral, × 1; **2**, apical, × 1; **3**, lateral, × 1; **5**, detail of peristomial region, × 2·5. Jebel Thanais, lowest 2 m of the Simsima Formation. **4,** BMNH EE4329, lateral, × 1. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation.

Figs 6–13 *Zuffardia morgani* (Cotteau & Gauthier). **6–8,** BMNH EE3789; **6**, oral; **7**, lateral; **8**, posterior, all × 2. Jebel Rawdah, section 2, bed 11. **9,** BMNH EE3791; apical, × 2. Jebel Rawdah, section 2, bed 21. **10–13,** Topotype specimen in the Morgan Collection, Museum d'Histoire Naturelle, Paris; **10**, apical; **11**, oral; **12**, posterior; **13**, lateral; all × 1·5. Senonian, Dah-e-Rouh Davl, Iran.

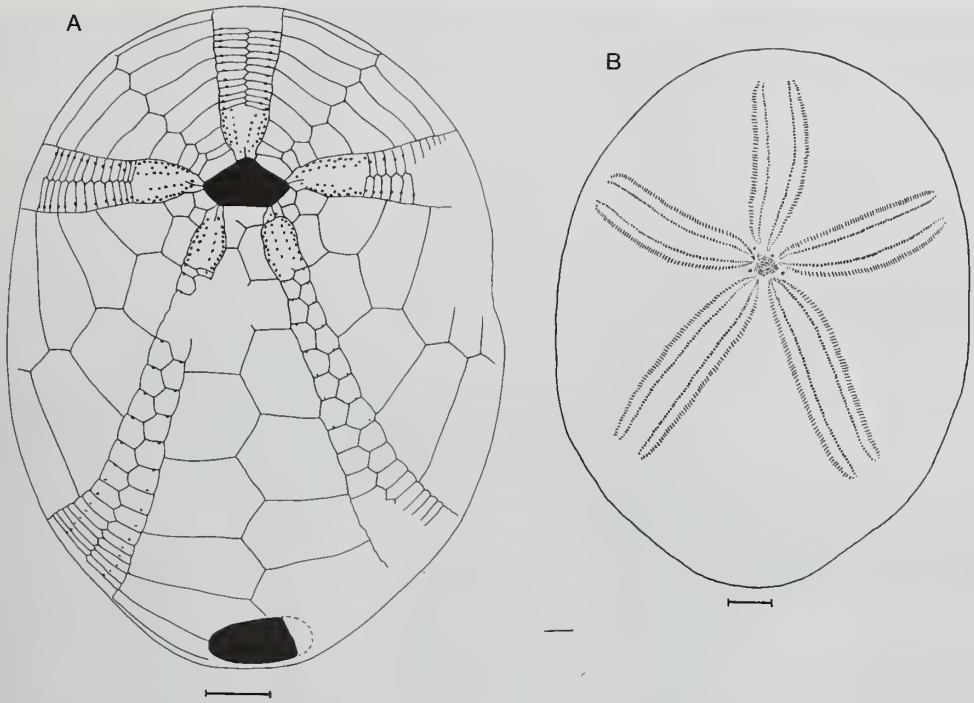


Fig. 50 Camera lucida drawings of *Vologesia rawdahensis* Ali. **A**, oral plating, BMNH EE3384; **B**, adapical plating, BMNH EE4326. Scale bars = 5 mm.

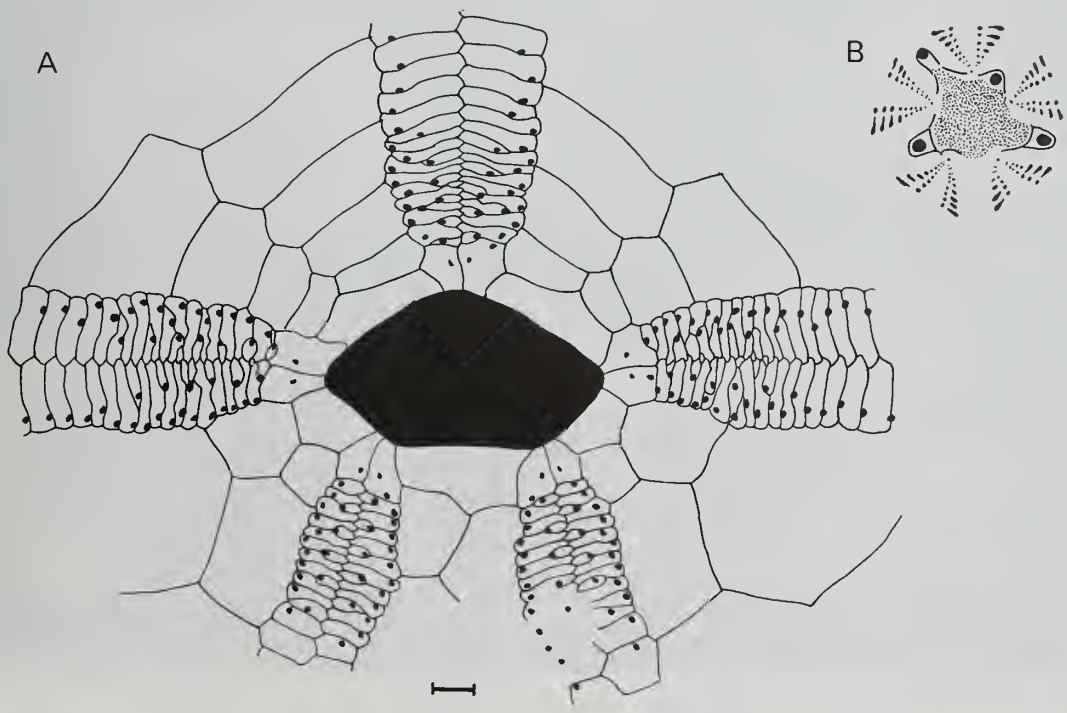


Fig. 51 Camera lucida drawings of *Vologesia rawdahensis* Ali. **A**, peristome and surrounding phyllodes, BMNH EE3384; **B**, apical disc plating, BMNH EE4326. Scale bar 1 mm.

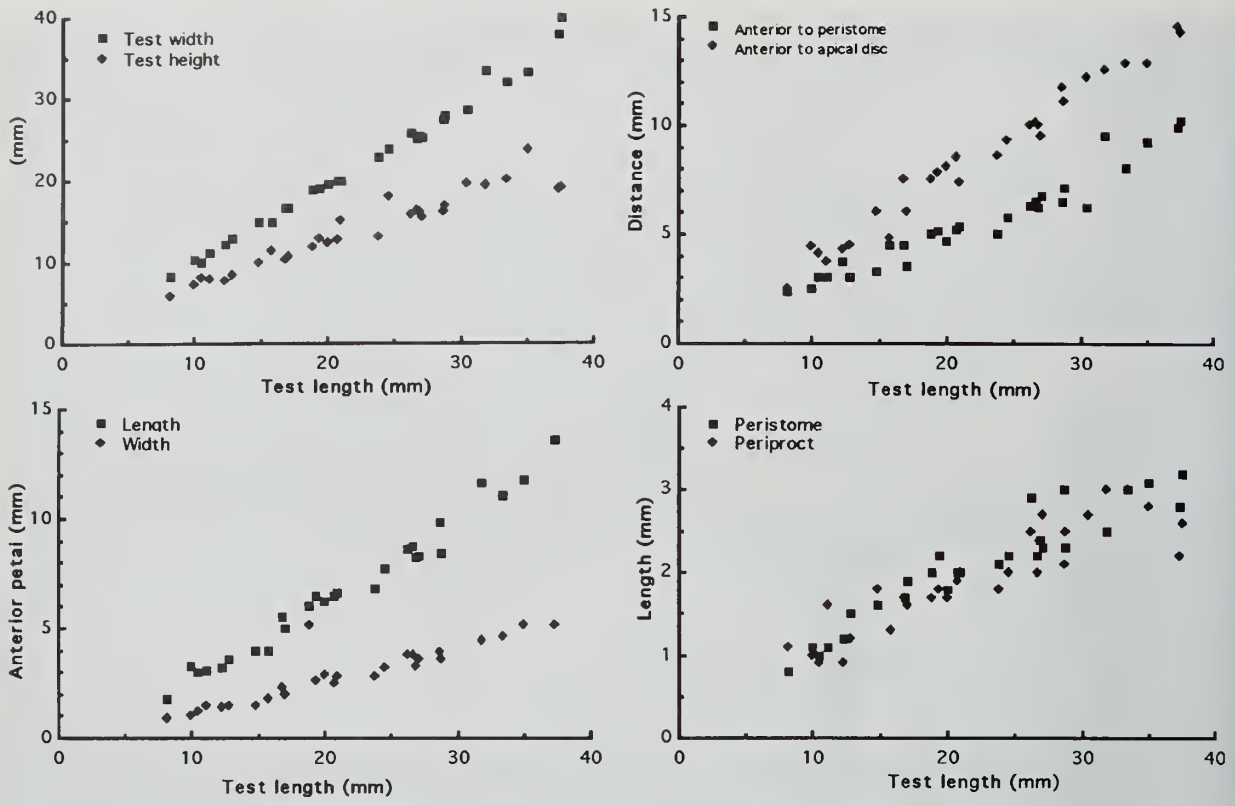


Fig. 52 Biometric data for *Faujasia eccentripora* Lees.

Faujasia eccentripora Lees, 1928 Pl. 22, figs 5–14; Figs 52–55

1928 *Faujasia eccentripora* Lees: 661, pl. 46, fig. 2.
1989 *Faujasia eccentripora* Lees; Ali: 403, fig. 4 (25).

TYPES. Holotype, BMNH E18347, paratypes BMNH E18344–46, E18348, from the late Cretaceous (?Maastrichtian) of Jebel el Malih, Oman.

MATERIAL STUDIED. 465 specimens were collected for study, of which 29 (BMNH EE3823, EE3825–26, EE3832–34, EE3836–39, EE3851, EE3855–61, EE3866–67, EE3872–76, EE3878–79, EE3882, EE3897) were measured for the biometric analysis given here.

OCCURRENCE. This species is known only from Oman and the United Arab Emirates. It occurs abundantly at the *Loftusia* levels at Jebel Huwayyah and in the lowest 8 m of calcarenitic limestones at Jebel Rawdah 2. Elsewhere it is rare. It was collected at the following localities and stratigraphic levels:
Jebel Aqabah: bed 1 (6, all juvenile).
Jebel Huwayyah, section 1: bed 9 (6); beds 10–11 (33).
Jebel Huwayyah, section 2: bed 3 (1).
Jebel Rawdah, section 1: top of bed 2 (5); top of bed 4 (2); loose in scree at base (6).
Jebel Rawdah, section 2: bed 4 (14); bed 5 (2); beds 6–8 (92); bed 10 (1); bed 11 (101); bed 14 (7); bed 16 (3); bed 19 (19); bed 20 (2); bed 21 (22); bed 22 (3); beds 23–25 (1); bed 25 (3); loose, from lower part of succession (beds 2–11) (112); loose in scree from higher part of succession (13).
Jebel Rawdah, section 3b: bed 2 (3); bed 8 (1); bed 9 (3).
Jebel Rawdah, section 4: bed 2 (1); bed 4 (2); beds 21–22 (1).

DESCRIPTION. Tests are shield-shaped in outline with a rounded anterior, a projecting pointed posterior and two marked angles coinciding with the posterior ambulacra (Pl. 22, figs 5–14; Fig. 53). Tests range in length from 8 to 37·5 mm. They have a rounded ambitus and slightly convex oral surface, with a marked sternal keel. The test is widest posterior of midlength and maximum width is 92–106% test length. The upper surface is low and rounded, never peaked. Test height is 50–77% of test length, being greatest in small individuals and progressively decreasing through growth (Fig. 52).

The apical disc lies 30–44% of test length from the anterior border (mean = 38%, N = 29). It is more central in larger forms. The disc is monobasal with the entire apical region occupied by the madreporite. There are four gonopores but these lie outside the apical disc, opening instead within the interambulacra and separated from the madreporite by one or two interambulacral plates (Fig. 54).

The petals are strongly inflated and closed distally, being widest at midlength (Pl. 22, figs 6, 10, 13; Fig. 53B). All five are similar in size and the anterior three extend some 70–80% of the way from the apex to the ambitus. Both pores in the pore-pair are circular or subcircular and united by a furrow. Pores are all single beneath the petals.

The peristome is small, only about 10% of the test length in diameter. It is rounded quinquestellate in outline and approximately as wide as broad. It lies 20–30% of the test length from the anterior border (mean = 25%, N = 29). The

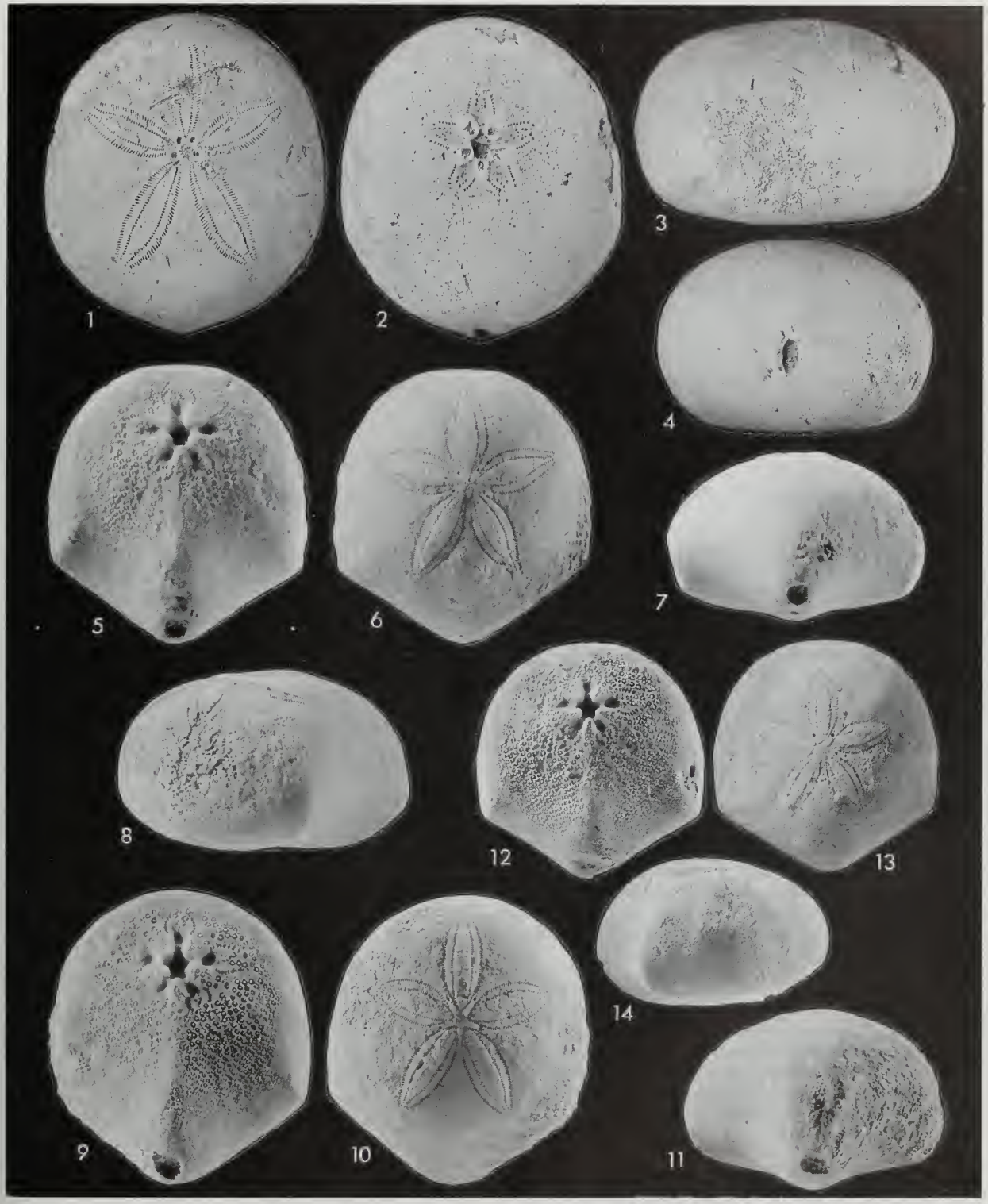


PLATE 22

Figs 1–4 *Zuffardia morgani* (Cotteau & Gauthier). BMNH EE4325; **1**, apical; **2**, oral; **3**, lateral; **4**, posterior; all × 2. Jebel Rawdah, section 1, bed 3.

Figs 5–14 *Faujasia eccentripora* Lees. **5–7**, BMNH EE3821; **5**, oral; **6**, apical; **7**, posterior; all × 2. Jebel Rawdah, section 2, bed 14. **8–11**, BMNH EE3826; **8**, lateral; **9**, oral; **10**, apical; **11**, posterior; all × 2. Jebel Rawdah, section 2, loose in scree at level of bed 14. **12–14**, BMNH EE3825; **12**, oral; **13**, apical; **14**, lateral; all × 2. Jebel Rawdah, section 2, bed 11.

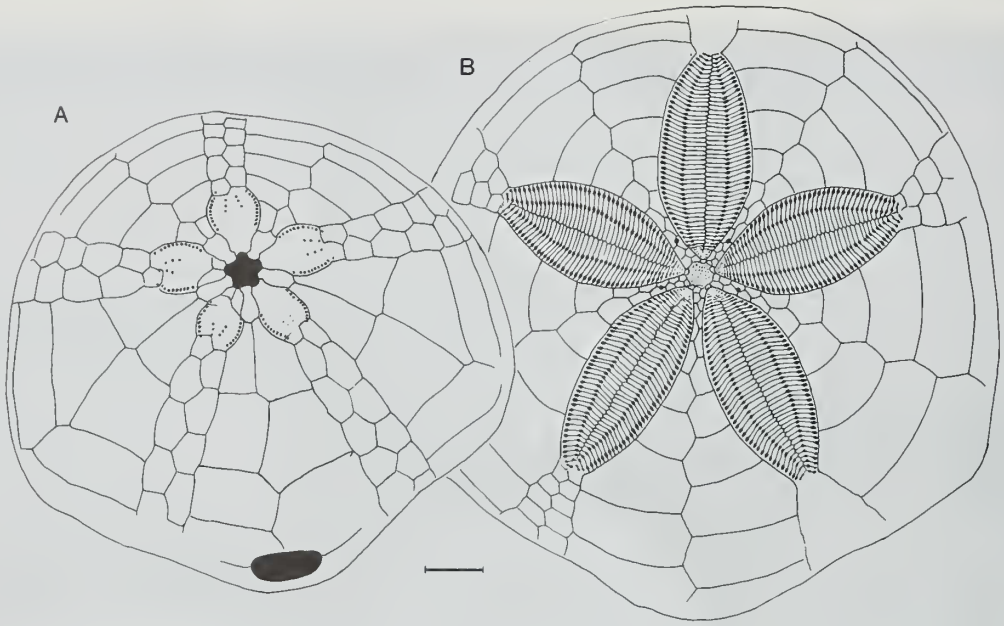


Fig. 53 Camera lucida drawings of *Faujasia eccentripora* Lees. **A**, BMNH EE3882, oral surface; **B**, BMNH EE3824, adapical surface. Scale bar = 5 mm.

basicoronal plates of the interambulacra are rather narrow and elongate (Fig. 55), as are the next two pairs of plates in the posterior three interambulacra (Fig. 54). The bourrelets are rather square-sided and blunt-ended and project strongly (Pl. 22, figs 5, 9, 12). The phyllodes are short and broad and are sunken. Pores are strongly arcuate with 8 to 12 pores in the outer series and only 2 or 3 in the inner series (Fig. 55). The inner series of pores are well separated from the peristome, but there are two pairs of sphaeridial pits adorally (Fig. 55). Miniscule buccal pores are present but are much smaller than other pores in the phyllodes and are clearly rudimentary only.

The periproct is small and circular, width being 85–122% of its length. It lies close to the posterior margin on the oral surface at the end of the sternal ridge and faces slightly posteriorly (Pl. 22, figs 7, 11).

Tuberculation is fine and uniform aborally and slightly coarser adorally. There is a narrow naked zone that extends from just posterior of the posterior bourrelet half way towards the periproct.

REMARKS. This species was first erected by Lees (1928) for specimens from Jebel el Malih, Oman. It differs from *Faujasia apicalis* Desor, from the Maastrichtian of Belgium, the Netherlands and France in a number of important respects. *F. apicalis* has shorter petals, a sharper ambitus and is more pointed apically in profile. Furthermore, its peristome is much less anterior and the oral surface is flatter and lacks such a pronounced sternal keel.

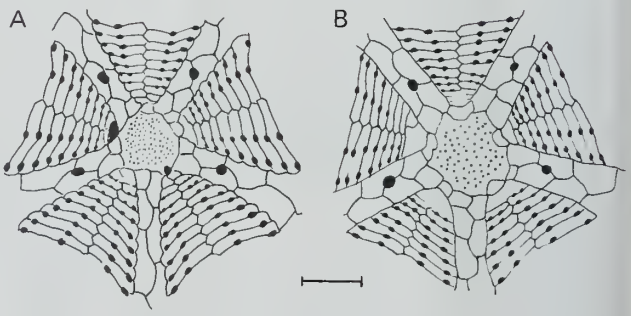


Fig. 54 Camera lucida drawings of apical disc plating of *Faujasia eccentripora* Lees. **A**, BMNH EE3824; **B**, BMNH EE3826. Scale bar = 1 mm.

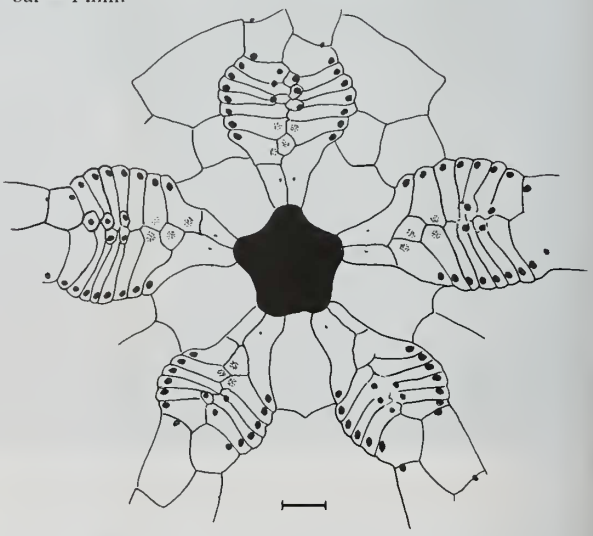


Fig. 55 Camera lucida drawing of phyllode plating in *Faujasia eccentripora* Lees, BMNH EE3902. Scale bar = 1 mm.

Genus *ZUFFARDIA* Checchia-Rispoli, 1917

TYPE SPECIES. *Pseudocatopygus sanfilippoi* Checchia-Rispoli, 1914, by original designation.

OTHER SPECIES INCLUDED. In addition to the type species, there are four nominal species, three of which have previ-

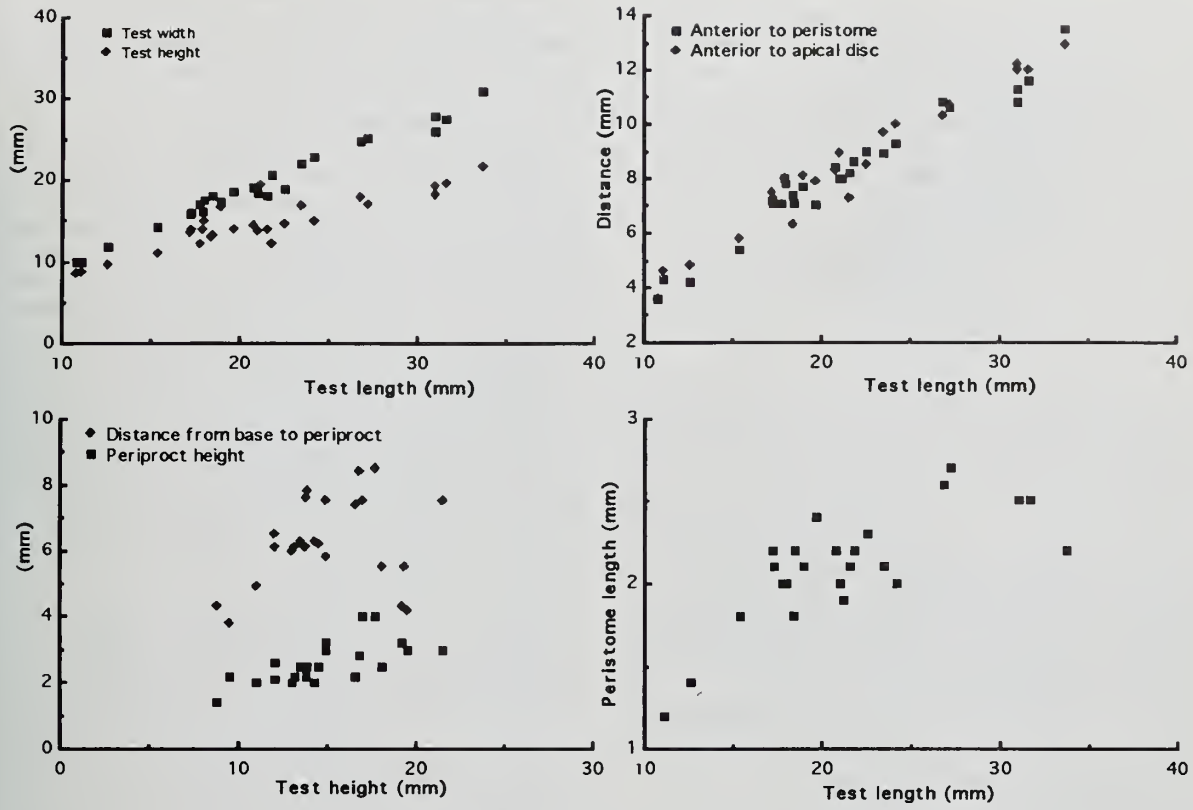


Fig. 56 Biometric data for *Zuffardia morgani* (Cotteau & Gauthier).

ously been assigned to this genus; *Catopygus rohlfsi* Krumbeck, 1906, *Catopygus boucarti* Lambert & Thièry, 1925, *Catopygus morgani* Peron & Gauthier, 1895, *Zuffardia creullii* Checchia-Rispoli, 1933. All are here treated as synonymous with *C. morgani*, the oldest available name.

Diagnosis. Oval test with a monobasal apical disc, broad petals of equal length, a posterior longitudinal periproct and a longitudinal peristome with short phyllodes and buccal pores.

Occurrence. The genus occurs in the late Cretaceous of North Africa and the Middle East. It is recorded from the Maastrichtian of Libya, Algeria and Oman and the United Arab Emirates, and from the upper Senonian (?Maastrichtian) of southern Iran.

Remarks. This genus resembles *Catopygus* Agassiz, 1836, in its general shape and form but differs from that genus in having a monobasal apical disc and single pores below the petals. It also appears rather similar to the Tertiary genus *Kephrenia* Fourtau, 1909, having very similar phyllodes and longitudinal peristome. It differs from *Kephrenia* in periproct shape, *Kephrenia* having a small transverse periproct as opposed to the longitudinal periproct of *Zuffardia*. It also shares many characteristics in common with *Faujasia*, including its phyllode and bourrelet structure, small periproct positioned low on the posterior face and apical disc plating. It differs from *Faujasia* in having gonopores confined to genital plates, and in being much more oval in shape.

Only two species are recognized here, the type *Z. sanfilippoi* and *Z. morgani* (Cotteau & Gauthier).

Zuffardia morgani (Cotteau & Gauthier, 1895) Pl. 21, figs 6–13; Pl. 22, figs 1–4; Figs 56–59

1895 *Pseudocatopygus Morgani* Cotteau & Gauthier: 60, pl. 9, figs 6–9.
?1906 *Catopygus Rohlfsi* Krumbeck: 87, pl. 7, fig. 4.
1914 *Pseudocatopygus rohlfsi* Krumbeck; Checchia-Rispoli: 301, pl. 1, fig. 3.
1925 *Catopygus boucarti* Lambert; Lambert & Thièry: 587, pl. 13, figs 6–9.
1933 *Zuffardia creullii* Checchia-Rispoli: 4, pl. 1, figs 1–4.
1939 *Catopygus boucarti* Airaghi: 258.
1981 *Zuffardia rohlfsi boucarti* (Lambert); Roman, in Amard *et al.*: 112.
1987 *Zuffardia* aff. *rohlfsi boucarti* (Lambert); Zhagbib-Turki: 257.
1989 *Zuffardia sanfilippoi* Ali: 406, fig. 5 (67).

Types. The holotype is the single specimen figured and described by Cotteau & Gauthier (1895). It has not been located. However, another specimen from the same locality and in the Morgan collection is figured here (Pl. 21, figs 10–13).

Material studied. Seventy one specimens were collected, of which 28 (BMNH EE3382–85, EE3531, EE3789–93, EE3796–804, EE3806, EE3808, EE3812–17, EE4325, EE5050) were used for the following biometric analysis.

Occurrence. The species occurs In Tunisia, Algeria and Libya as well as in southern Iran and the United Arab Emirates and Oman. It is apparently restricted to the Maas-

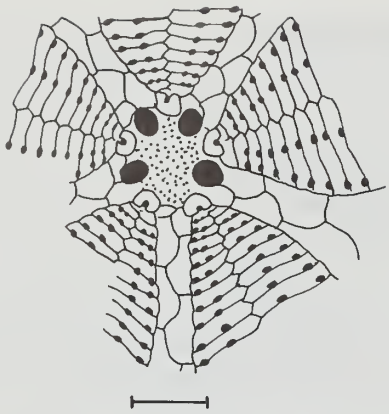


Fig. 57 Camera lucida drawing of apical disc plating in *Zuffardia morgani* (Cotteau & Gauthier), BMNH EE3791. Scale bar = 1 mm.

trichtian. In the study area described here, the species is found only at Jebel Rawdah, at the following localities:
Jebel Rawdah, section 1: bed 3 (5).
Jebel Rawdah, section 2: bed 11 (47); bed 19 (5); bed 21 (5); bed 25 (1); loose, mostly derived from beds 2–11 (48).
Jebel Rawdah, section 4: bed 2 (1).

DIAGNOSIS. A species of *Zuffardia* with a rather flat base and a periproct that becomes progressively more adoral as test size increases. Test shape highly variable, either inflated, keeled or depressed.

DESCRIPTION. Tests ovoid in shape ranging from 10·8 to 33·7 mm in length. In plan view they are rounded anteriorly and slightly pointed posteriorly (Pl. 21, fig. 9). The ambitus is rounded and in profile the base is flattish and the upper surface ranges from low-domal or even flat, to conical and pointed at the apex (Pl. 21, fig. 7; Pl. 22, fig. 3). Test width is 83–97% of the length (mean = 90%, N = 25) and test height 55–91% of the length (mean = 71%, smaller individuals being proportionately taller, Fig. 57).

The apical disc is monobasal and positioned 33–47% of the test length from the anterior border (mean = 40%, N = 24; Fig. 56). The madreporite is large and its pores extend to, and partially enclose, the four gonopores (Fig. 57). There appears to be a distinct sexual dimorphism in gonopore size, with large individuals having either large, closely spaced gonopores some 0·3–0·5 mm in diameter (female?) and others of comparable size having only small (0·1 mm diameter) gonopores (male?).

Petals are lanceolate and converge distally but do not close (Pl. 22, fig. 1; Fig. 58B). Petals II, III and IV are about 70–80% the length of the posterior petals. The two pores in each pair are approximately circular and connected by a groove. The three anterior petals extend approximately 70% of the distance to the ambitus, the posterior pair only some 60% or so. In middle to large individuals the interporal zone is 1·0–1·5 times as broad as an individual pore zone. Pores below the petals are all single.

The peristome is pentagonal in outline and slightly longer than wide (length is 1·2–1·5 times its width; mean = 1·3). It lies 33–38% of test length from the anterior border. Phyllodes are short and arcuate, with two series of pores in each column (Fig. 59). There are 6 or 7 pores in the outer series and only 1 or 2 in the inner series. There are also two pairs of sphaeridial pits in each half ambulacrum situated perradially. A small number of occluded plates are developed and buccal pores are present. The phyllodes are not depressed but remain flush with the test. The bourrelets project outwards strongly but do not indent the peristome (Pl. 21, fig. 6; Pl. 22, fig. 2).

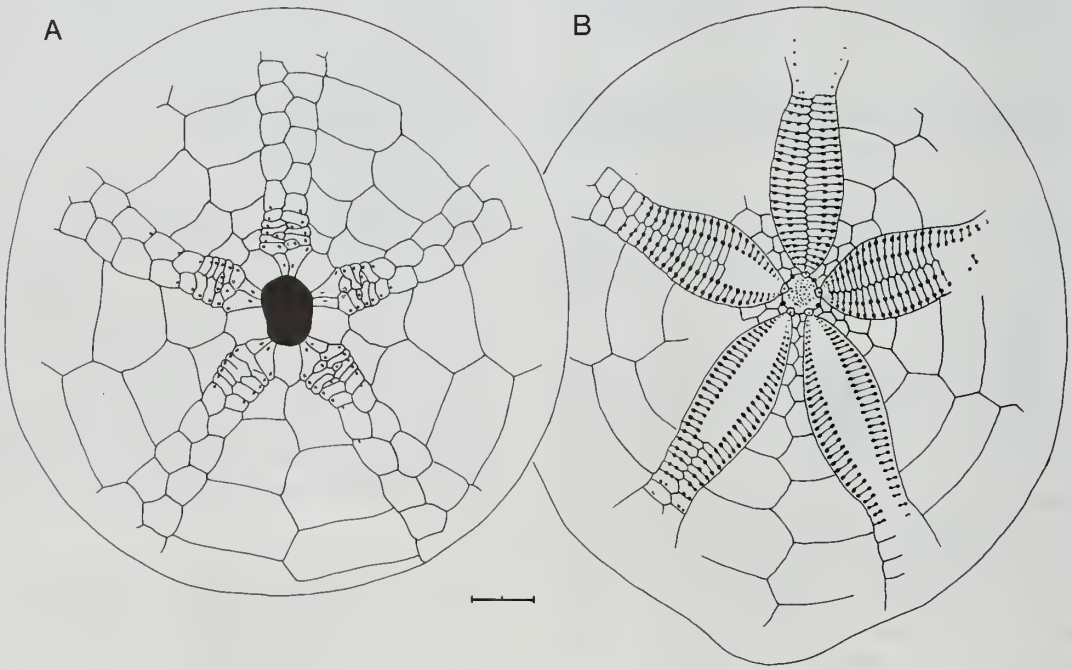


Fig. 58 Camera lucida drawings of plating in *Zuffardia morgani* (Cotteau & Gauthier). **A**, BMNH EE3385, oral plating; **B**, BMNH EE3384, adapical plating. Scale bar = 2 mm.

The periproct lies on the posterior face, relatively high in juveniles but becoming progressively lower in larger specimens (Fig. 56). The base of the periproct lies 50% of test height above the base in small individuals, but can lie as low as 22% of test height in the largest individuals. There is, however, considerable variation in the height of the periproct within the sample. The periproct is relatively small and taller than wide (height = 1·3–2·5 times greater than width). Typically, there is a slight adapical projection and rim developed around the periproct.

Tuberculation is fine and uniform aborally and slightly coarser adorally. There is a narrow sternal naked zone on the oral surface behind the peristome.

REMARKS. This species was first described from the 'Upper Senonian' (probably Maastrichtian) of Derre-i-Chahr, southern Iran, by Cotteau & Gauthier (1895: 60) under the name *Catopygus morgani*. Cotteau & Gauthier distinguished it from other similar species by its inflated shape and convex oral surface. Although their figure indicates a peristome that is as broad as long, in all other respects it falls exactly within the range of the United Arab Emirates population described here (Fig. 57). Should the Iranian population prove to have a consistently more equant peristome, then it clearly should be treated as a distinct species. However, the figures cannot be considered entirely reliable and this difference is not apparent in topotype material (Pl. 21, figs 10–13). Consequently, for the present the two forms are synonymized.

In 1906 Krumbeck erected the species *Catopygus rohlfsi* on the basis of a specimen from the late Cretaceous of Libya. Closely comparable material from Algeria was given the name *Catopygus boucarti* by Lambert & Thièry (1925). Based on a large collection of specimens from the Maastrichtian of Libya, Airaghi (1939) was later able to synonymize Lambert's *Catopygus boucarti* and Krumbeck's *Catopygus rohlfsi*. The large populations of *Zuffardia boucarti* Lambert, described from Algeria by Roman (in Amard *et al.* 1981) also fall within the range of the material described here, though they do not achieve a size greater than about 2 cm (Libyan specimens cover an identical range to the population described here).

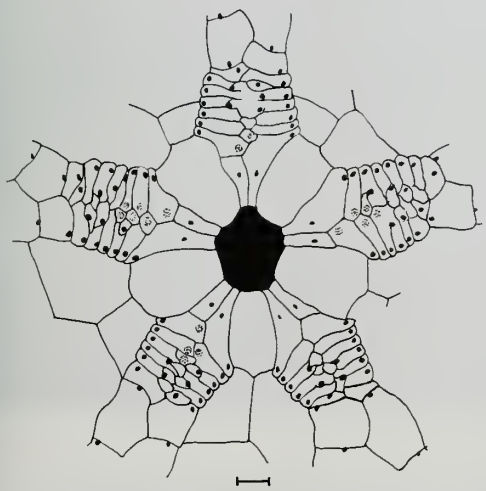


Fig. 59 Camera lucida drawing of adoral plating of *Zuffardia morgani* (Cotteau & Gauthier), BMNH EE4325. Scale bar = 1 mm.

Thus there can be little doubt that these populations are all synonymous. However, there remains slight doubt over whether Krumbeck's original specimen is conspecific. Roman (in Amard *et al.* 1981) pointed out that Krumbeck's (1906) original figure shows a specimen whose apical disc lies well displaced towards the anterior and whose periproct is shown as being visible from above. I suspect that this is simply due to the Krumbeck's specimen being slightly crushed and distorted, or possibly simply being illustrated from an oblique angle. But the type specimen has not been located and thus the validity of this species must remain uncertain.

In 1914 Checchia-Rispoli described a more spherical form with a strongly inflated oral surface under the name *Pseudocatopygus sanfilippoi*. There are three specimens, the largest of which is 42 mm in length. This form has a much higher periproct than is found in my populations (Fig. 57), and corresponds to the juvenile positioning (as does the more spherical test shape). This lies well outside the range of form found in *Z. morgani* from either the Algerian or the United Arab Emirates populations, and clearly represents a distinct species. Checchia-Rispoli (1917) made this the type species of his new genus *Zuffardia*.

The only other species assigned to *Zuffardia* is *Z. creullii* Checcia-Rispoli (1933). This is based on a single individual 33 mm in length that corresponds to a more inflated variant of *Z. morgani*. Biometrically it falls more or less within the range of variation encountered in the population described here. It too, therefore, is synonymized with *Z. morgani*.

Unnamed Family
Genus ***PYGUROSTOMA*** Cotteau & Gauthier, 1895

TYPE SPECIES. *Pygurostoma morgani* Cotteau & Gauthier, 1895, by original designation.

OTHER SPECIES INCLUDED. None.

OCCURRENCE. Late Cretaceous of Iran and the Oman Mountains.

DIAGNOSIS. Large, oval and rather flattened cassiduloid with a narrow, elongate and invaginated inframarginal periproct. Peristome quinquestellate and subcentral with strong phyllodes containing many occluded plates and pores. Buccal pores present, well separated from the peristome. Apical disc tetrabasal and subcentral. Petals long and well developed, converging distally. Naked zone on the oral area between the peristome and periproct, and also extending anterior of the peristome in ambulacrum III.

REMARKS. Kier (1962) included *Pygurostoma* in the family Faujasiidae on account of its phyllode structure. However, as Kier pointed out, this genus is rather different from other Faujasiidae. In particular the appearance of the periproct, which is strongly rostrate adapically and invaginated adorally, indicates that it is probably derived from a form with a posterior elongate periproct and weak anal canal. This is very different from the periproct seen in *Faujasia* and most other faujasiids. In test shape, peristome position and size, floscelle development, petal form and the distribution of naked zones, *Pygurostoma* undoubtedly comes closest to *Parapygus* Pomel, 1883. *Parapygus* has a narrow, vertically elongate periproct that lies posteriorly and in large forms is just visible adorally. Although many species have just two columns of pores in each half ambulacrum of the phyllodes, the type

species, *P. cotteauanus* (d'Orbigny) has a median zone of pores also. Thus, in many respects *Pygurostoma* is no more than an hypertrophic form of *Parapygus* in which the phyllodes have increased numbers of median pores and the periproct is inframarginal rather than marginal.

Only one other species was included in this genus by Kier (1962), *Pygurostoma pasionensis* Cooke, 1949, from the late Cretaceous of Guatemala. However, this species has its periproct flush with the test and not invaginated. I suspect this is not cogeneric.

Pygurostoma morgani Cotteau & Gauthier, 1895 Pl. 23, figs 1–4, 7; Figs 60–63

1895 *Pygurostoma morgani* Cotteau & Gauthier: 52, pl. 8, figs 1–5.
1962 *Pygurostoma morgani* Cotteau & Gauthier; Kier: 135, pl. 19, figs 1–3, text-fig. 117.
1992 *Pygurostoma morgani* Cotteau & Gauthier; Ali: 72, fig. 4.

TYPES. The whereabouts of Cotteau & Gauthier's specimens is unknown. A topotype specimen from the Morgan collection is illustrated (Pl. 23, fig. 1).

MATERIAL STUDIED. Forty specimens, of which 15 (BMNH EE3291–92, EE3296, EE3302–10, EE3315, EE3317, EE3322) were measured.

OCCURRENCE. The species was first described from the 'Upper Senonian' of Aftab, Louristan, southern Iran. In this study specimens were most common in the lowest few metres of the Simsima limestones. Fifty specimens were collected or noted at the following localities and horizons:

Jebel Buhays, section 1: loose in the scree, derived from the lowest few metres of Simsima Formation (26).
Jebel Buhays, section 2: loose in scree, derived from lowest 2 m of the Simsima Formation (2).
Jebel Thanais: lowest 2 m of Simsima Formation (1).
Jebel Huwayyah, section 1: beds 14/15 (3).
Jebel Rawdah, section 2: bed 14 (3); bed 18 (1); bed 19 (2); bed 21 (7); bed 26 (2); loose in scree (1).
Jebel Rawdah, section 4: bed 19 (1).
Jebel Faiyah, section 1 (southern tip): bed 8 (1).

DIAGNOSIS. As for genus.

DESCRIPTION. Tests are oval in outline with a rounded anterior and slightly pointed and projecting posterior (Pl. 23, figs 1–3). In profile the test is low domal with a rounded ambitus and slightly angled posterior (Pl. 23, fig. 4). The oral surface is concave towards the peristome. Test length ranges from 55 to 95 mm. Test width is 65–81% of test length (mean = 76%, N = 15), test height 35–47% of test length (mean = 40%).

The apical disc lies 37–44% of test length from the anterior border. It is tetrabasal (Fig. 62), with genital plates 1, 2 and 4 reduced to minute plates largely occupied by the gonopores. The madreporite is stellate in form.

Petals are long and weakly lanceolate in outline (Fig. 61). The anterior petal and the two posterior petals are similar in length, being 35–42% of the test length. The latero-anterior petals are shorter, typically 80–90% of the length of the other

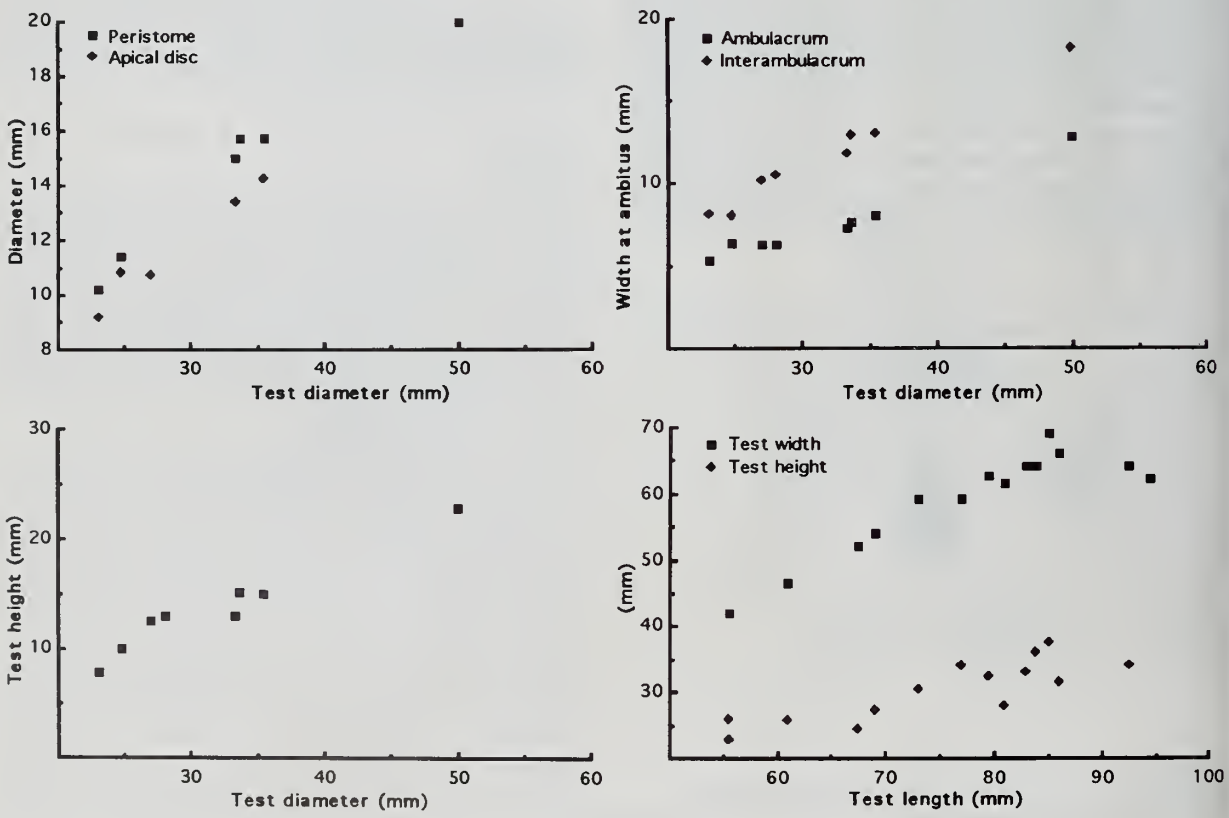


Fig. 60 Biometric data for *Pygurostoma morgani* Cotteau & Gauthier.

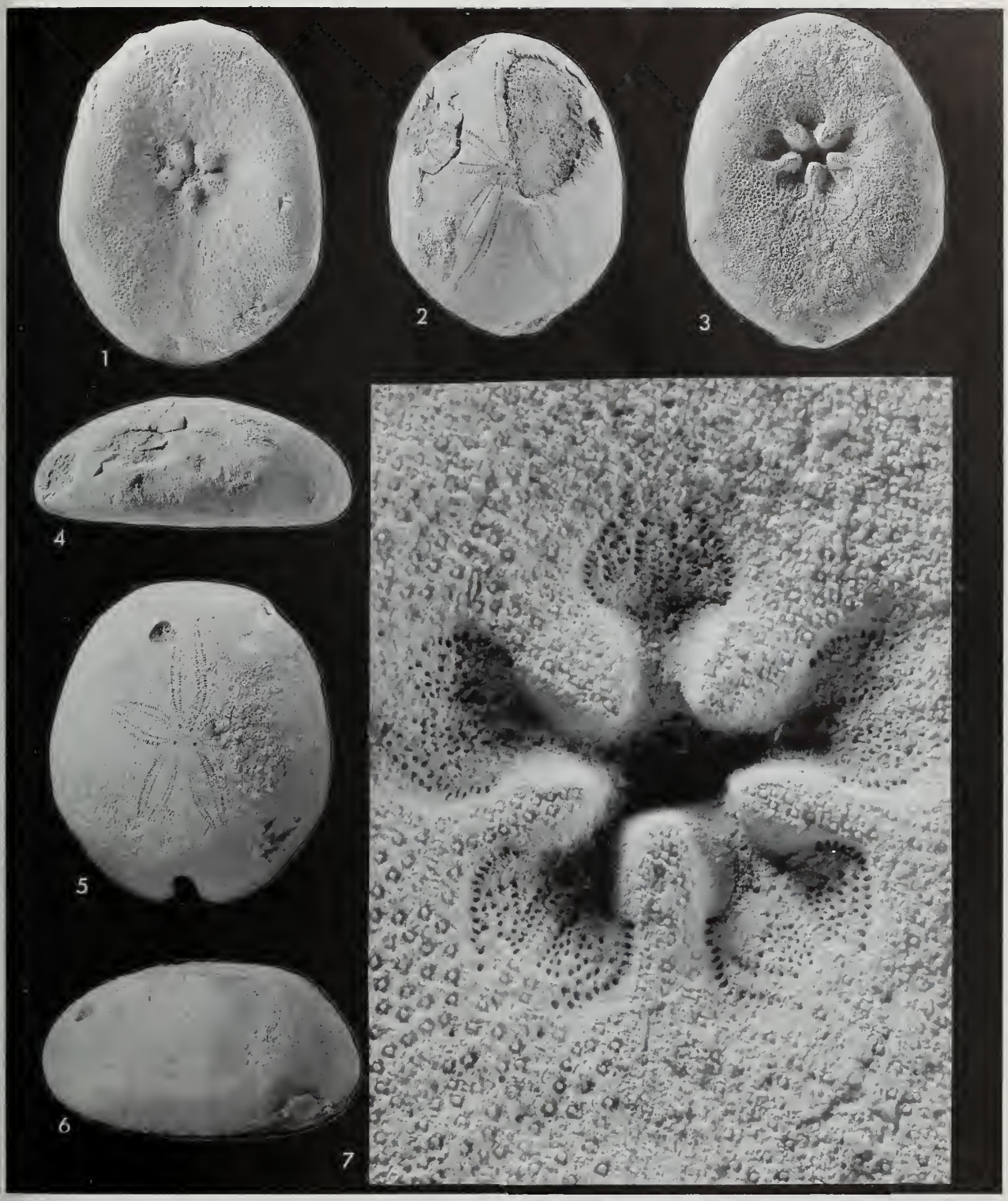


PLATE 23

Figs 1–4, 7 *Pygurostoma morgani* Cotteau & Gauthier. **1**, specimen in the Morgan Collection, Museum d'Histoire Naturelle, Paris; oral, × 1. Senonian of Iran; no locality details. **2–4, 7**, BMNH EE3315; **2**, apical, × 0·9; **3**, oral, × 1; **4**, lateral, × 1; **7**, detail of peristome × 6. Jebel Rawdah, section 2, loose in scree at level of bed 12.

Figs 5, 6 *Petalobrissus linguiformis* (Peron & Gauthier). BMNH EE4318; **5**, apical; **6**, lateral; both × 2. Jebel Rawdah, section 2, bed 21.

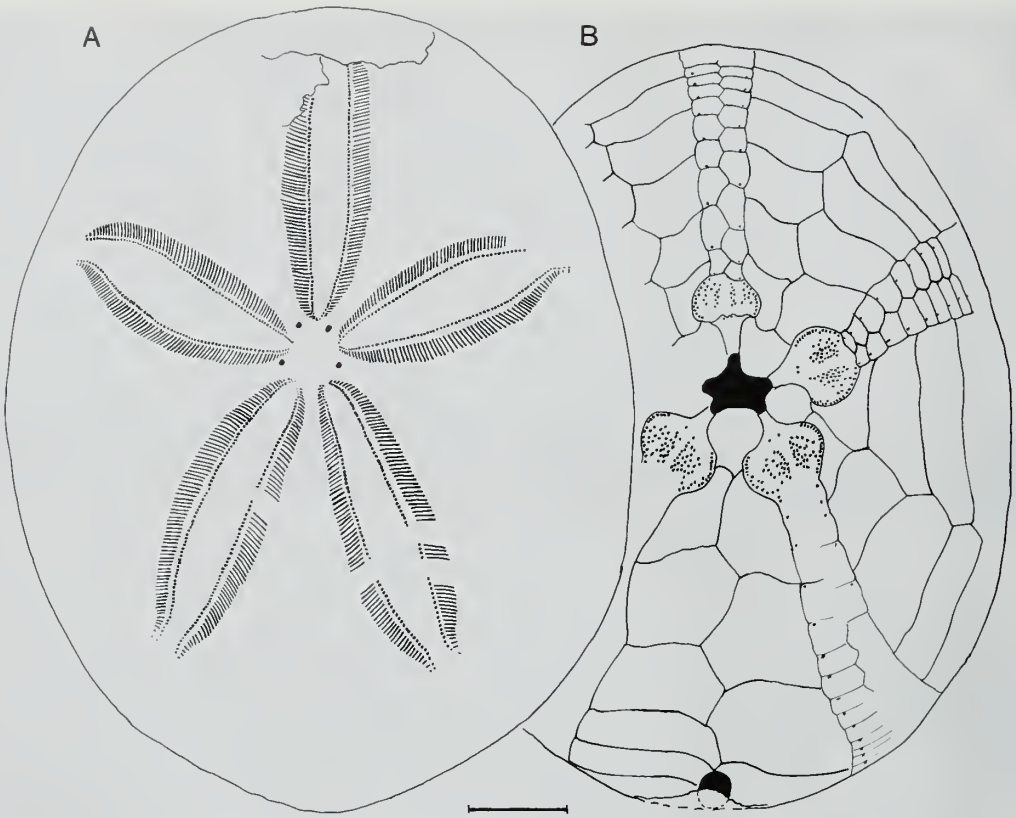


Fig. 61 Camera lucida drawings of plating in *Pygurostoma morgani* Cotteau & Gauthier. **A**, BMNH EE3303, apical; **B**, BMNH EE3304, oral. Scale bar = 1 cm.

three. The anterior petal is also typically narrower and more parallel-sided than the other petals. The two pores are subcircular and widely separated, united by a well developed groove. The petals converge slightly distally but do not close (Fig. 61). The interporal zone is about twice the width of a single pore zone. Pores below the petals are all single.

The peristome is quinquestellate in outline with the prominent bourrelets projecting into the opening (Pl. 23, fig. 7). The bourrelets are triangular and have long lateral bands of fine tuberculation. They are blunt-ended. The phyllodes are distinctly sunken and arcuate. They consist of many rows of pores (Fig. 63). There is a well defined outer series and inner series in each half ambulacrum, but the central zone consists of a broad band of unorganised pores, four or five abreast. The anterior ambulacrum, however, has notably fewer median pores than other ambulacra, with only one or two median pores abreast. There are 16–18 pores in the outer series and 7 or 8 in the inner series. There are many occluded plates in the phyllodes (Fig. 63). The peristome is 1·4 to 2·1 times as wide as it is long and is situated 33–43% of test length from the anterior border (mean = 39%, N = 13).

The peristome is small and lies inframarginally, typically forming a small pointed rostrum. There is a distinct, well-formed invagination of the test on the adoral margin of the periproct but not adambitally. The periproct is oval and longer than wide (width = 45–70% of length). It opens between interambulacral plates 6 and 8 (Fig. 61).

Tuberculation is fine and dense aborally, slightly less fine and less dense adorally. There is a very pronounced fusiform naked zone along the sternum between the peristome and periproct. This is slightly raised above the surrounding test and is covered in small pits. There is a similar, smaller naked zone developed anterior of the peristome in ambulacrum III.

REMARKS. The species was described and figured by Cotteau & Gauthier (1895). In the same work they described a number of smaller species of *Parapygus* under the name *Pseudocatopygus*. Some of these may possibly turn out to be juveniles of *P. morgani*.

This species is very different from the only other possible species assigned to this genus, *P. pasionensis* Cooke (1949), from the ?Campanian of Guatamala. *P. pasionensis* has much less well developed bourrelets and its periproct is more equant and lies completely flush and is not invaginated. As discussed above, it is not clear that *P. pasionensis* is congeneric with *P. morgani*.

Family **CASSIDULIDAE** Agassiz & Desor, 1847
Genus ***PETALOBRISSUS*** Lambert, 1916

Petalobrissus rawdahensis sp. nov. Pl. 24, figs 1–12; Figs 64, 65

TYPES. Holotype, BMNH EE3485; paratypes, BMNH EE3467–84, EE3486–87, EE4321–22.

OTHER MATERIAL. Over 650 specimens were collected.

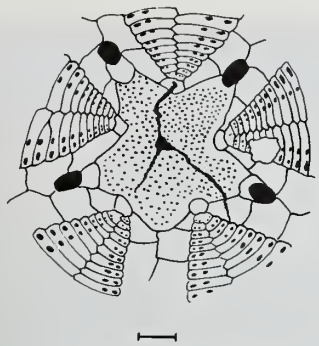


Fig. 62 Camera lucida drawing of apical disc plating in *Pygurostoma morgani* Cotteau & Gauthier, BMNH EE3288. Scale bar = 1 mm.

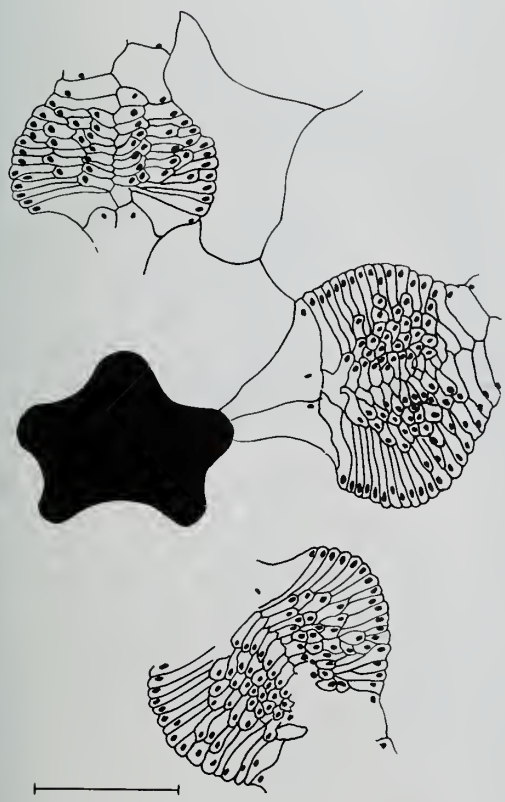


Fig. 63 Camera lucida drawing of phyllode plating in *Pygurostoma morgani* Cotteau & Gauthier, BMNH EE3304. Scale bar = 5 mm.

OCCURRENCE. This species occurs abundantly at Jebel Rawdah, section 2 but is found virtually nowhere else. The only other occurrence of this species is in the lowest bed (bed 1) at Jebel Rawdah, section 3b. At section 2 the species is found at the following levels: bed 4 (3); bed 8 (4); bed 11 (247); bed 12/13 (230); bed 14 (17); bed 15 (25); bed 19 (73); beds 20–21 (45); bed 22 (13); bed 26 (2). Additional material was collected loose from the scree at this locality.

DIAGNOSIS. A *Petalobrissus* with a monobasal apical disc and a small quinquestellate peristome, anterior in position and surrounded by small pointed bourrelets. Phyllodes well-developed, composed of outer and inner series of pores. Buccal pores present. Periproct posterior, longitudinal. Narrow, smooth tubercle-free zone present both anterior and posterior to the peristome. In outline the posterior projects slightly and adorally there is a characteristic interradial keel in the posterior interambulacrum.

DESCRIPTION. Tests are oval in outline, uniformly rounded at the anterior, but slightly pointed posteriorly (Pl. 24, figs 5, 6). Test length ranges from 10·3 to 21·2 mm. Test width is 88–95% of test length (mean = 91%, SD = 1·8%, N = 23) and the widest point is slightly posterior of midlength. In profile the test is depressed with a relatively flat upper surface, a uniformly rounded anterior and an obliquely truncated posterior (Pl. 24, figs 4, 7, 10, 11). The tallest point coincides with the apical disc or is slightly posterior to it. The ambitus is rounded and relatively low. Test height is 51–62% of test length (mean = 56%, SD = 2·4%, N = 23; Fig. 64). The oral surface is flat anteriorly, but slopes away towards the posterior. There is a relatively sharp and well-defined posterior keel on the oral surface along the midline and two less sharply defined keels in the two postero-lateral interambulacra (Pl. 24, figs 5, 8).

The apical disc lies 37–46% of test length from the anterior border (mean = 43%, SD = 2·5%, N = 23). It is monocyclic, with four gonopores that open at around 10–13 mm test length. The gonopores are oval and there is no sign of any suture separating them from the central area of madrepores (Fig. 65C). Ocular plates are small and subtriangular in outline.

Petals are bowed and converge distally, though remaining open (Fig. 65A). The anterior petal is the longest and the least bowed. It has about 20 pore-pairs in a column at test length of 10 mm, rising to 39 at 21 mm test length. The perradial portion of the ambulacrum is about 1·5 times the width of a single pore zone. Lateral and posterior petals are 60–86% of the anterior petal in length and are more strongly bowed. In all petals the two columns are of equal length. The posterior petals end well short of the periproct.

All pores below the petals are single. The phyllodes are well developed and strongly bowed but are only slightly sunken (Pl. 24, figs 1, 5, 12). The first ambulacral plates are elongate and bootshaped in outline, with small buccal pores (Fig. 65D). There is an outer series of closely packed pores and a shorter inner series of equally closely spaced pores (Pl. 24, fig. 12; Fig. 65D). There are 10 or 11 pores in the outer series of lateral and posterior phyllodes, and 9 or 10 in ambulacrum III. There are 4 or 5 pores in the inner series in all ambulacra. Despite the large number of individuals available, none show the detailed plating of the phyllode region adequately. The outer series of pores lie on a series of narrow plates that do not reach the perradius. Internally there is a second series of plates housing the inner series of pores. These may be oblique, but in no specimen is the plating in this region clear.

The peristome is pentagonal, slightly broader than long in larger individuals, and situated 33–39% test length from the anterior border (mean = 36%, SD = 1·5%, N = 23). The peristome width is 7–12% of test length and its length is 85–100% of its width. The peristome is sunken with well developed vertical walls. The surrounding interambulacral areas are developed into short, projecting, knob-like bourrelets, which do not, however, impinge on the peristome (Pl. 24, fig. 12).

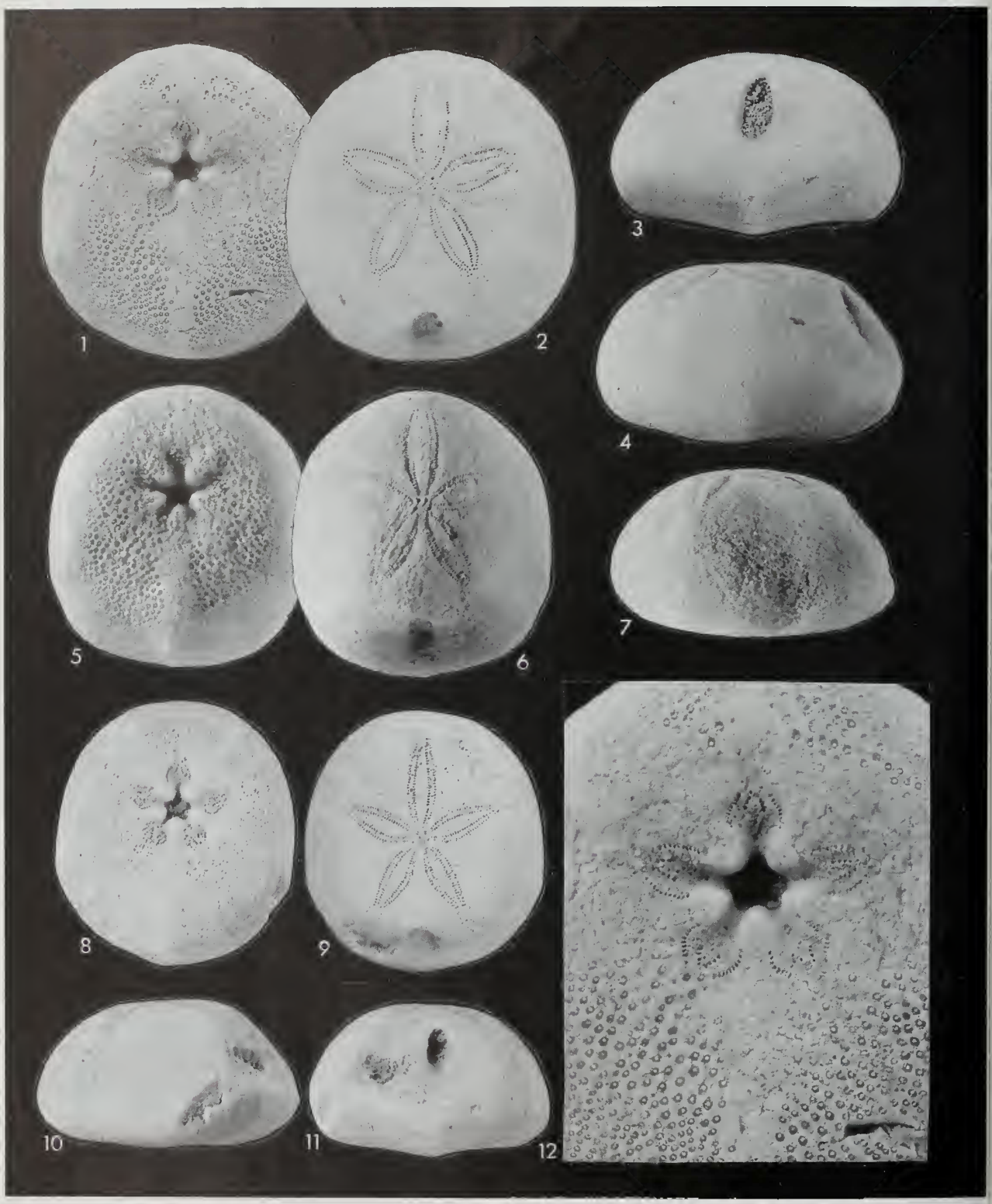


PLATE 24

Figs 1–12 *Petalobrissus rawdahensis* sp. nov. **1–4, 12,** BMNH EE4321, holotype; **1**, oral; **2**, apical; **3**, posterior; **4**, lateral; all × 3; **12**, detail of peristomal region, × 6. Jebel Rawdah, section 2, loose in scree at level of bed 11. **5–7**, BMNH EE3485, paratype; **5**, oral; **6**, apical; **7**, lateral; all × 3. Jebel Rawdah, section 2, bed 11. **8–11**, BMNH EE4322, paratype; **8**, oral; **9**, apical; **10**, lateral; **11**, posterior; all × 3. Jebel Rawdah, section 2, loose in scree at level of bed 11.

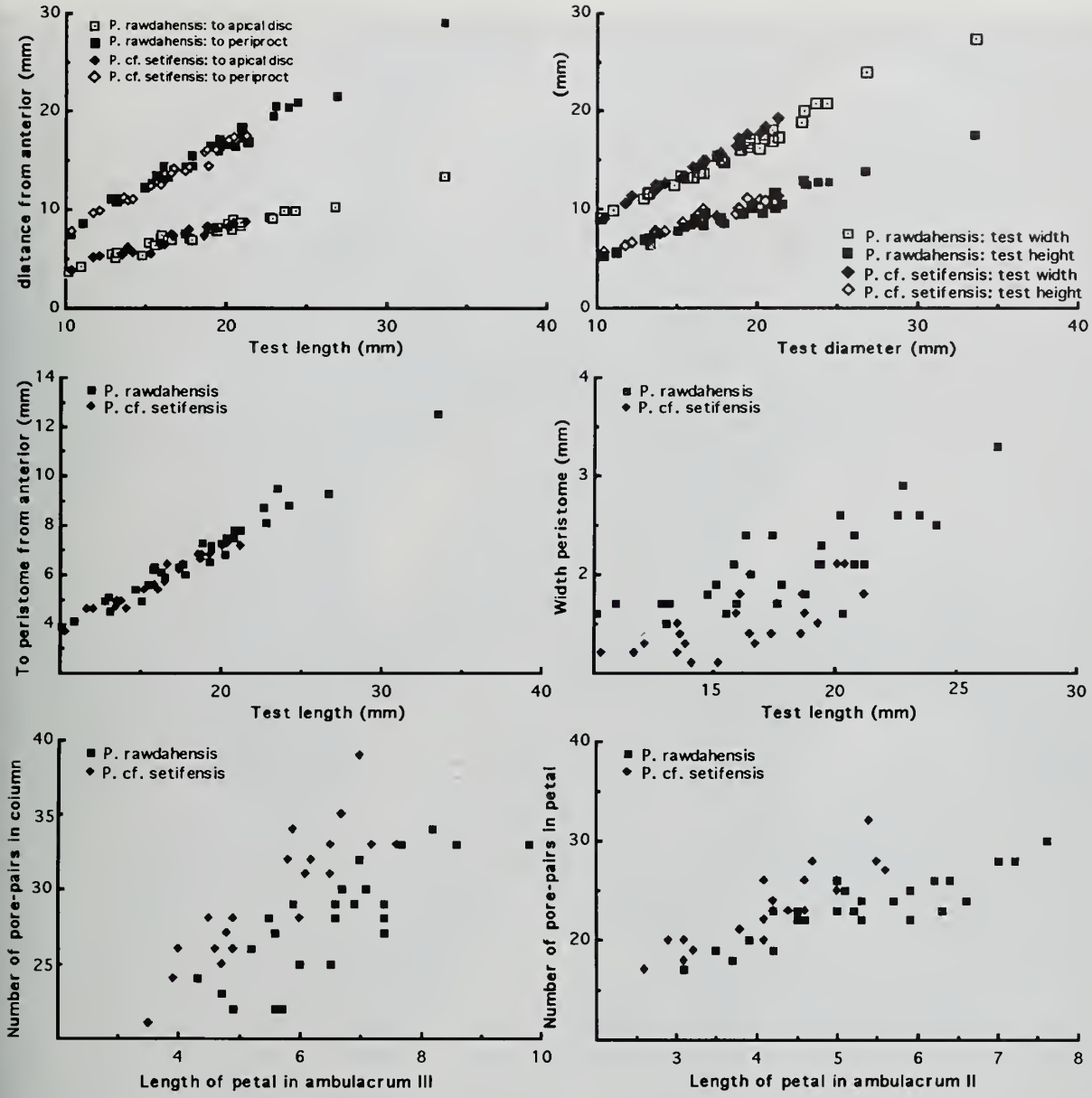


Fig. 64 Biometric data for *Petalobrissus rawdahensis* sp. nov. and *P.* cf. *setifensis* (Cotteau).

The periproct is clearly visible from above and opens 77–87% test length from the anterior border (mean = 82%, SD = 2·7%, N = 23). It is longitudinal, with a width that is 41–65% of its height. The opening is near vertical, with slightly invaginated walls forming a short, parallel-sided anal sulcus. There is a subanal rostrum (Pl. 24, figs 2, 6, 9–11).

Tuberculation is fine and uniform aborally, slightly coarser adorally. On the oral surface there is a narrow band free of tubercles down the midline of the posterior interambulacrum. This is finely granular and tapers towards the posterior.

Remarks. This species is problematic to place on account of its monobasal apical disc. In general shape and plating it conforms closely to species of *Petalobrissus*, having very similar phyllodes and bourrelets, a similar longitudinal periproct set far back on the test, and only a remnant anal sulcus. However, the type species of *Petalobrissus* has a tetrabasal apical disc according to Kier (1962), whereas *P. rawdahensis* has a monobasal disc. *P. rawdahensis* also bears a strong resemblance to small *Hardouinia* species, especially in the characteristic keeled oral surface, bowed petals and well developed bourrelets. However, in the type species of *Hardouinia*, *H. mortonis*, the phyllodes are more strongly arcuate with the inner series arranged distally as an integral part of the arc. Furthermore, the peristome opens subcentrally. In the type species of *Procassidulus*, *P. lapiscancri* (Goldfuss) from the Maastrichtian of Maastricht, the phyllodes are less arcuate and the inner series is parallel to the outer series of pores. *P. rawdahensis* also differs from *P. lapiscancri* (Goldfuss) in being larger, more rounded in profile and oval in outline, and in having more pores in its

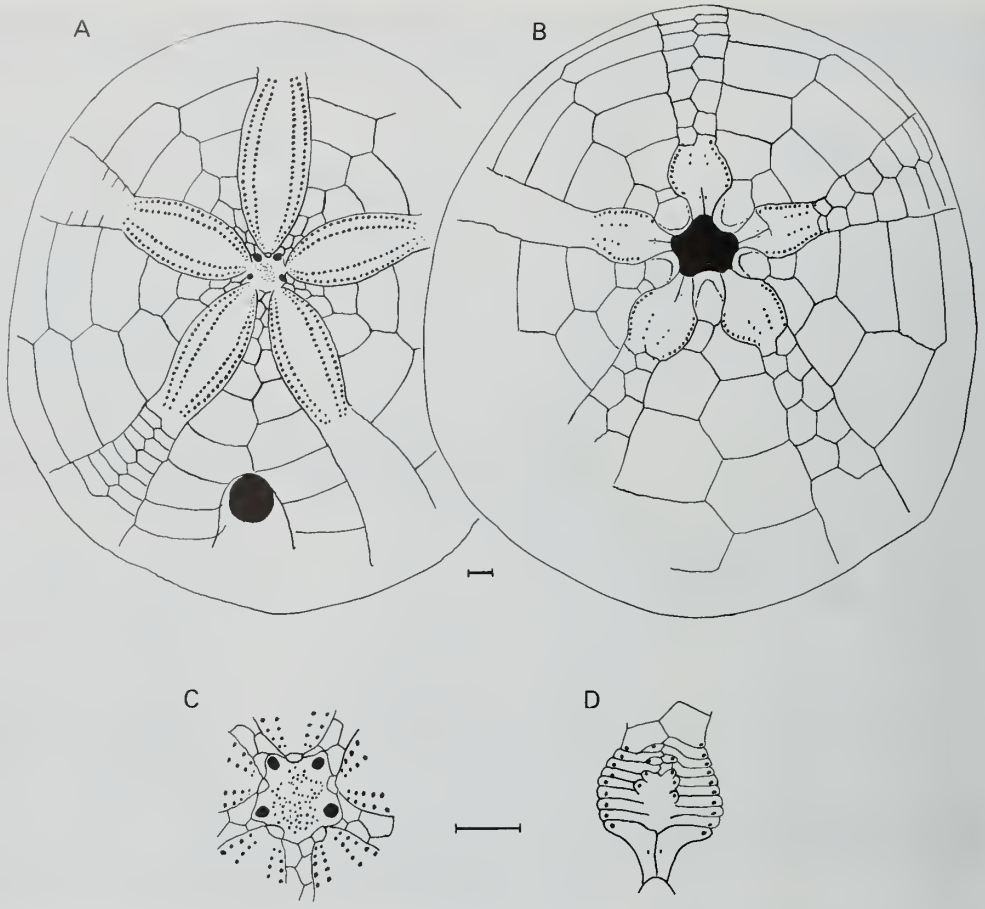


Fig. 65 Camera lucida drawings of plating in *Petalobrissus rawdahensis* sp. nov. **A**, apical surface, BMNH EE3485; **B**, oral surface, BMNH EE3487; **C**, apical disc, BMNH EE3476; **D**, One phyllode, peristome margin at base, BMNH EE3484. Scale bars = 1 mm.

phyllodes at comparable sizes. Pending revision of this group, *P. rawdahensis* is placed in the genus *Petalobrissus*.

Petalobrissus rawdahensis is easily distinguished from *Petalobrissus* cf. *setifensis* (Peron & Gauthier), which occurs in the same section, by its more angular outline, its posterior keel and slope on the oral surface, its smaller, less quinquelobate peristome and its more bowed and densely pored petals.

Petalobrissus* cf. *setifensis (Cotteau, 1866) Pl. 25, figs 1–10; Figs 64, 66

cf. 1866 *Echinobrissus setifensis* Cotteau: 267, pl. 14, figs 13–15.
cf. 1962 *Petalobrissus setifensis* (Cotteau); Kier: 125, pl. 16, figs 10–13.
1989 *Petalobrissus inflatus* Gauthier & Thomas; Ali: 405, fig. 5 (9).

Material studied. Thirty one specimens were used for the biometric analysis: BMNH EE3505–10, EE3512–28, EE3530, EE3532, EE3535, EE3537–41. An additional 269 specimens were collected.

Occurrence. Apart from five specimens collected from the scree at Jebel Buhays, section 1, and a single specimen from bed 9 at Jebel Bu Milh, all the material comes from sections at Jebel Rawdah. The distribution of specimens is as follows:
Jebel Rawdah, section 1: bed 3 (18).
Jebel Rawdah, section 2: bed 8 (9); bed 11 (124); beds 12/13 (4); bed 14 (15); bed 19 (23); bed 21 (44); bed 26 (3).
Jebel Rawdah, section 3b: bed 2 (4).
Jebel Rawdah, section 4: bed 4 (1); beds 8/9 (3).

Description. Tests are oval in outline, uniformly rounded at the anterior and slightly flattened at the posterior (Pl. 25, figs 1, 2). Test length ranges from 10 to 33 mm. Test width is 82–93% of test length (mean = 87%, SD = 2·9%, N = 31), with the widest point slightly posterior of midlength. Test height is 49–61% of test length (mean = 54%, SD = 3·1%, N = 31), with the highest point at or a little posterior of the apical disc. In profile the anterior is uniformly rounded, the posterior obliquely truncated (Pl. 25, figs 4, 10). The ambitus is rounded and about one-quarter of the test height above the base. The oral surface is flat, with a very slight depression towards the peristome.

The apical disc lies 37–48% test length from the anterior border (mean = 42%, SD = 2·4%, N = 31) being relatively more anterior in larger individuals (Fig. 64). It is monocyclic with no evidence of any sutures between the gonopores and central madreporite region in any specimen, even where ocular plate sutures are clear (Fig. 66D). However, the

PLATE 25

Figs 1–10 *Petalobrissus* cf. *setifensis* (Cotteau). **1, 10,** BMNH EE4341; **1**, oral; **10**, lateral; both × 3 Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation. **2–5,** BMNH EE3519; **2**, apical; **3**, oral; **4**, lateral; **5**, posterior; all × 3. Jebel Rawdah, section 2, bed 11. **6–9,** BMNH EE3536; **6,** apical; **7**, oral; **8**, lateral; **9**, posterior; all × 3. Jebel Rawdah, section 2, bed 19.

Figs 11, 12 *Arnaudaster cylindriformis* sp. nov. BMNH EE4324, depressed variety; **11**, oral; **12**, apical; both × 2 (see also Pl. 29, Figs 6, 9). Jebel Rawdah, section 2, in scree at level of bed 14.

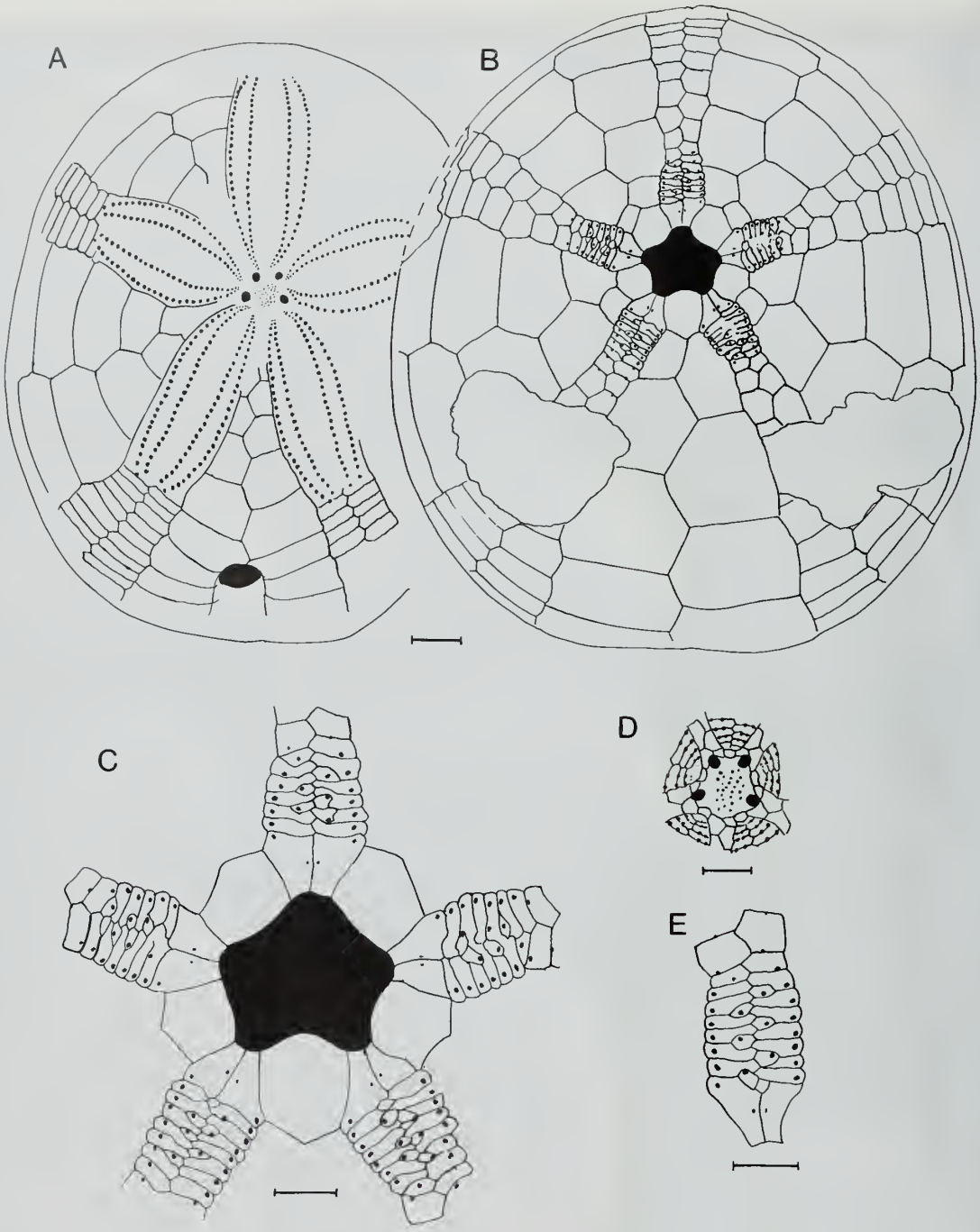


Fig. 66 Camera lucida drawings of plating in *Petalobrissus* cf. *setifensis* (Cotteau). **A**, apical surface, BMNH EE3514; **B**, oral surface, BMNH EE3535; **C**, phyllode plating, BMNH EE3524; **D**, apical disc, BMNH EE3524; **E**, single phyllode, peristome margin to base, BMNH EE3535. Scale bars: A, B = 2 mm, C-E = 1 mm.

madrepores do not usually extend up to the gonopores. Gonopore diameter varies markedly between individuals of the same test length, indicating sexual dimorphism in this species. Gonopores appear at around 10–12 mm test length.

Petals are lanceolate, with almost straight lines of inner pores and only slightly bowed lines of outer pores in all petals (Pl. 25, fig. 2; Fig. 66A). All are distally open and both inner and outer pores are subcircular in outline. The anterior petal is the longest and has about 22 pore-pairs in a column at 15 mm test length, rising to 39 at 33 mm test length. Petals in ambulacra II and IV are 65–93% of the length of the anterior petal (mean = 80%, SD = 6·6%, N = 28), whereas the posterior petals are 73–100% of the length of the anterior petal (mean = 87%, SD = 6·6%, N = 28). The posterior

petals end well short of the periproct.

All pores below the petals are single. The phyllodes are only slightly expanded and are flush with the surrounding test (Pl. 25, figs 1, 3). Irrespective of size there are 7 or 8 pores forming an outer series and 3 or 4 pores forming an inner series in the phyllodes (Figs 66C, E). The first ambulacral plates are boot-shaped and carry small buccal pores, but are not particularly elongate. The inner series of pores are found on small occluded plates which are separated from one another (i.e. they do not form a continuous inner series of plates). Each is separated from its neighbours by two of the outer plates. Sphaeridial pits are confined to the area between the most adoral of the inner series of pores and the buccal pores. There are just two or three in each column.

The peristome is quinquelobate, and relatively large (Fig. 66C). Its length is 9–16% of the test length (mean = 11%, SD = 1·6%, N = 29) and 81–120% of its width. There is a distinct vertical-walled well to the peristome, covered in fine miliary tubercules. Bourrelets are not developed. However, the interambulacral margins to the peristomial well are elevated slightly, forming a lip-like rim (Pl. 25, fig. 1).

The periproct is longitudinal and clearly visible from above (Pl. 25, figs 2, 6). It lies 76–92% of test length from the anterior border (mean = 85%, SD = 3·5%, N = 31). It is about twice as tall as wide (mean width = 48% of height). There is a short parallel-sided anal sulcus that stops short of the ambitus.

All tubercles are sunken, those adorally being noticeably larger than the aboral ones. There is a median naked zone on the oral surface in both the anterior ambulacrum and the posterior interambulacrum (Pl. 25, figs 1, 3, 7). The anterior zone is short and does not reach the ambitus, but the posterior zone is broader, approximately parallel-sided and reaches the posterior border. It is finely granular.

REMARKS. This species could at first glance be confused with *Petalobrissus rawdahensis*, but is distinguished on several counts. It has a larger, more quinquelobate peristome, a flatter base without the posterior keel, it lacks bourrelets and has less inflated phyllodes with fewer pores. It has more parallel-sided petals with less densely packed pore-pairs. It resembles certain other species of *Petalobrissus* in its overall shape and form, but is distinguished by its monobasal apical disc. In particular it most closely resembles *P. cubensis* (Weisbord), particularly in its floscelle structure. However, it differs from *P. cubensis* in having a narrower posterior naked zone on its oral surface, in having its apical disc less anterior and in having a proportionally longer anterior petal.

It also comes close to certain species currently assigned to *Rhynchopygus* in test shape and floscelle structure, but differs in having a longitudinal rather than a transverse peristome. It is closest to *P. setifensis* (Peron & Gauthier), from the Maastrichtian of Algeria, but differs in some minor details, having a flatter base and more quadrate outline with less rounded ambitus, and in having fewer inner-series pores.

This species was identified by Ali (1989) as *Petalobrissus inflatus* (Gauthier & Thomas), but *P. inflatus* is a Cenomanian species that differs in several respects, notably in having much longer and more densely pored petals at equivalent sizes. These petals are strongly bowed in *P. inflatus* and the posterior pair extend back to a point level with the opening of the periproct.

Cassidulus oldhamianus Stolizcka, from the Maastrichtian Arrialoor Group of Southern India may be comparable, and appears similar in overall form. However, that species is inadequately described and figured and no examples of it are available for comparison. At present it is impossible to say what genus the species belongs to.

Petalobrissus linguiformis (Peron & Gauthier, *in* Cotteau, Peron & Gauthier, 1881) Pl. 23, figs 5, 6; Pl. 26, figs 1–6; Figs 67, 68

TYPES. Syntypes are the two measured specimens in the Peron & Gauthier collections referred to in Cotteau *et al.* (1881: 162).

MATERIAL STUDIED. Ten specimens, BMNH EE3334–35, EE3337, EE3341–45, EE4319, EE5021, were measured for the biometric analysis. An additional 11 specimens were also collected.

OCCURRENCE. This species was originally described from the Maastrichtian of Algeria, and has since been reported from Tunisia and Egypt. Apart from one specimen collected loose at Jebel Buhays, section 3, all specimens come from Jebel Rawdah. It is found at the following localities and horizons:

Jebel Buhays, section 1: loose in the scree, derived from the lowest few metres of the Simsima Formation (1).

Jebel Rawdah, section 2: bed 14 (4); bed 19 (5); bed 20 (1); bed 21 (4); loose from upper part of section (beds 14–21) (5).

Jebel Rawdah, section 4: loose in scree (1).

DIAGNOSIS. An elongate *Petalobrissus* with a narrow, almost vertical periproct and short anal sulcus set very far towards the posterior on the upper surface. Phyllodes are very strongly developed, with prominent bourrelets and outer and inner series of pores forming well-defined lines. There are up to 20 pores in the outer series and 10 in the inner series. In addition there are well developed rows of sphaeridial pits down the perradius.

DESCRIPTION. Tests are ovoid in outline, uniformly rounded at the anterior and slightly more pointed towards the posterior, with a slight, but distinct, anal cleft (Pl. 26, figs 1, 2). Tests range in size from 13 to 50 mm in length. The widest point on the test lies about two-thirds the distance from the anterior border. Test width is 76–87% of test length (mean = 82%, SD = 4·6%, N = 10). In profile the test is depressed, with a height that is 43–48% of test length (mean = 46%, SD = 1·8%, N = 9). The upper surface is slightly domed with the tallest point slightly posterior to the apical disc. The ambitus is uniformly rounded and lies at about one-third test height. The posterior is more or less truncated (Pl. 23, fig. 6).

The apical disc lies 34–44% test length from the anterior border (mean = 40%, SD = 3·0%, N = 7). It is tetrabasal, with a large madreporite plate and three small genital plates projecting into the interambulacra (Fig. 68D). These genital plates are U-shaped because of the gonopore that opens along their outer margin. Genital plates lie separated from adjacent ocular plates.

Petals are well developed (Pl. 26, fig. 5: Fig. 68B). The anterior and posterior pair of petals are both rather straight and remain open distally, whereas the antero-lateral pair of petals are more bowed and converge distally (Pl. 23, fig. 5). The perradial zone is about twice the width of a pore zone. The anterior petal is noticeably longer than other petals and extends more than three-quarters of the distance to the ambitus. Petals II and IV are 61–74% of the length of the

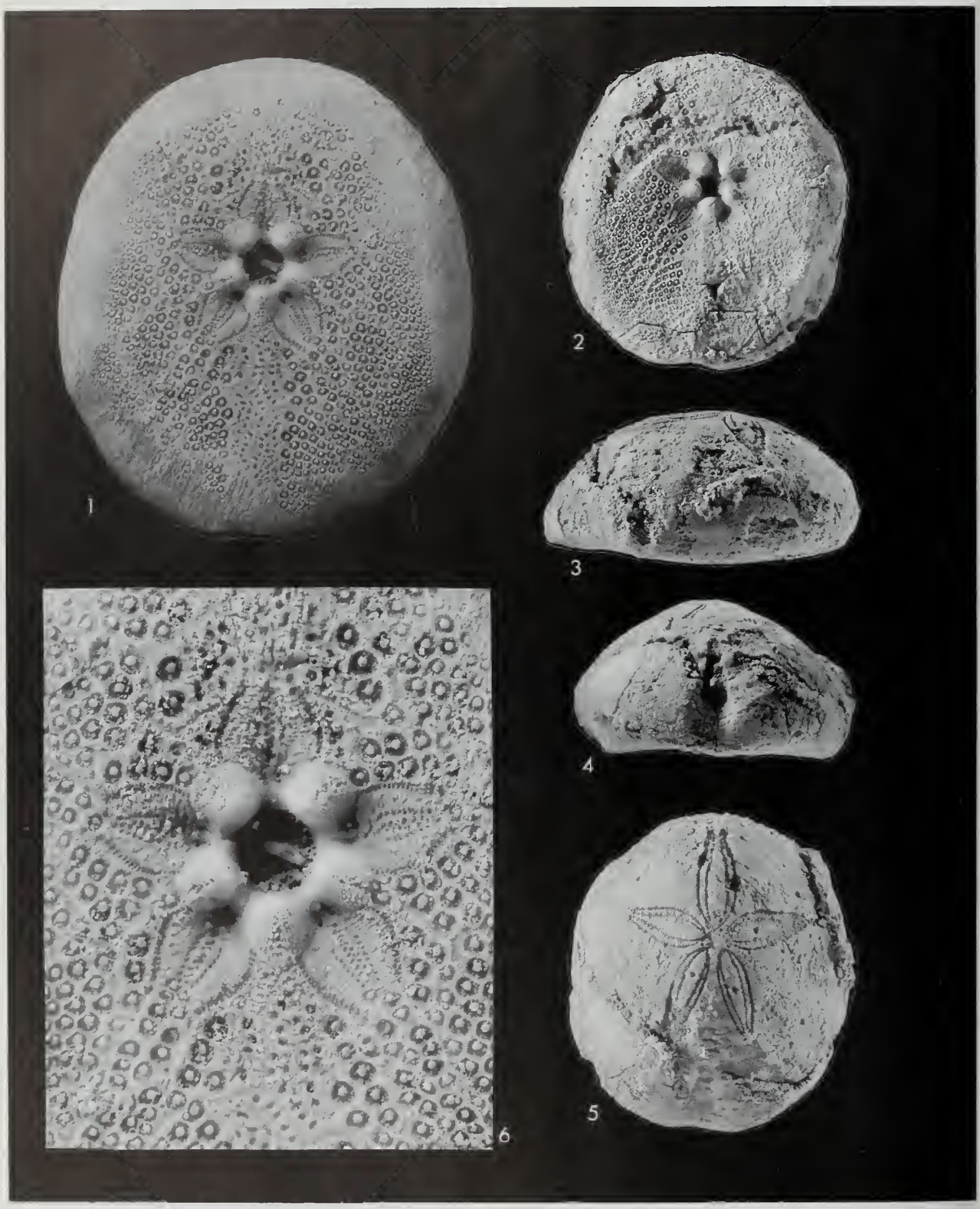


PLATE 26

Figs 1–6 *Petalobrissus linguiformis* (Peron & Gauthier). **1**, **6**, BMNH EE4319; **1**, oral, × 3; **6**, detail of peristome, × 6. Jebel Rawdah, section 2, beds 19/20. **2–5**, BMNH EE3345; **2**, oral; **3**, lateral; **4**, posterior; **5**, apical; all × 2. Jebel Rawdah, section 2, loose, derived from beds 14–21.

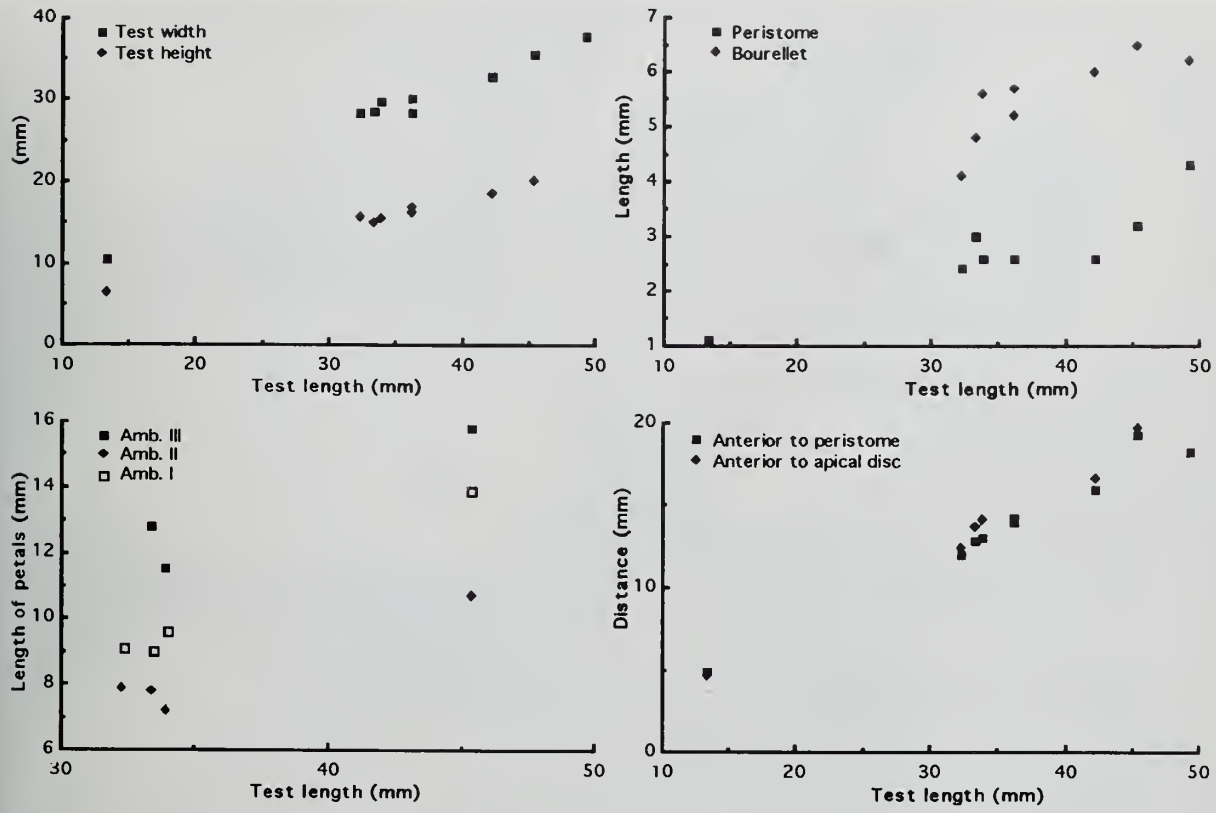


Fig. 67 Biometric data for *Petalobrissus linguiformis* (Peron & Gauthier).

anterior petal, wheras petals I and V are 71–89% of the length of the anterior petal. The posterior petal extends less than two-thirds the distance from the apical disc to the periproct.

All pores below the petals are single. The phyllodes are well developed and bow outwards strongly towards the peristome. They become slightly sunken towards the peristome, with the buccal pores situated in a shallow depression separated from the peristomial well (Pl. 26, fig. 6). There are two series of pores, well separated from each other and with pores closely packed together in each row. The outer row comprises some 17 to 20 pores, the inner series 7 to 9 (Fig. 68C). The first ambulacral plates are squat and broad, with buccal pores situated near their adambital edge and well separated from the peristome. Pores in the outer series are bowed and every third plate is smaller and does not reach the inner series of plates. These pores may be slightly offset, marking the incipient development of a median series of pores. The inner series of pores are situated towards the outer edge of a double column of occluded plates. Each plate carries a sphaeridial pit on its perradial side, there being some 8–10 sphaeridial pits forming a well defined column on either side of the perradial suture.

The peristome is subcircular to pentagonal and is approximately as broad as it is wide. It is 69% of test length in diameter and lies 37–42% of test length from the anterior border. There are short, pointed bourrelets which project outwards but do not impinge on the peristome (Pl. 26, fig. 6).

The periproct lies close to the posterior border, and is clearly visible from above (Pl. 26, fig. 5). It is longitudinal, being 27–40% as wide as it is tall (Pl. 26, fig. 4). It is slightly V-shaped, narrowing adapically, and opens into a short anal sulcus with parallel-sided walls. The periproct is almost vertical in orientation.

Tubercles are minute and densely packed aborally, but coarser and less dense adorally. There is a relatively broad naked zone in the posterior interambulacrum that runs from the peristome to the posterior border. This is 13–18% of the test width in width. It is covered in a reticulate pattern of pits.

Remarks. This species is readily differentiated from other cassiduloids described here by its highly developed phyllodes, its almost posterior periproct and its characteristic shape. The only species that come close are the southern Indian *P. testudo* (Forbes) and *P. emys* (Stoliczka), both from the Maastrichtian. Both have a similar test shape, with the posterior slit-like periproct, the anal notch and the projecting bourrelets. *P. testudo* has much less developed phyllodes with few pores in the inner series and only 8–10 pores in its outer series. *P. emys* is too poorly known to be compared closely as the original figures and description omit many important details such as phyllode structure. It may eventually prove to be synonymous with *P. testudo*.

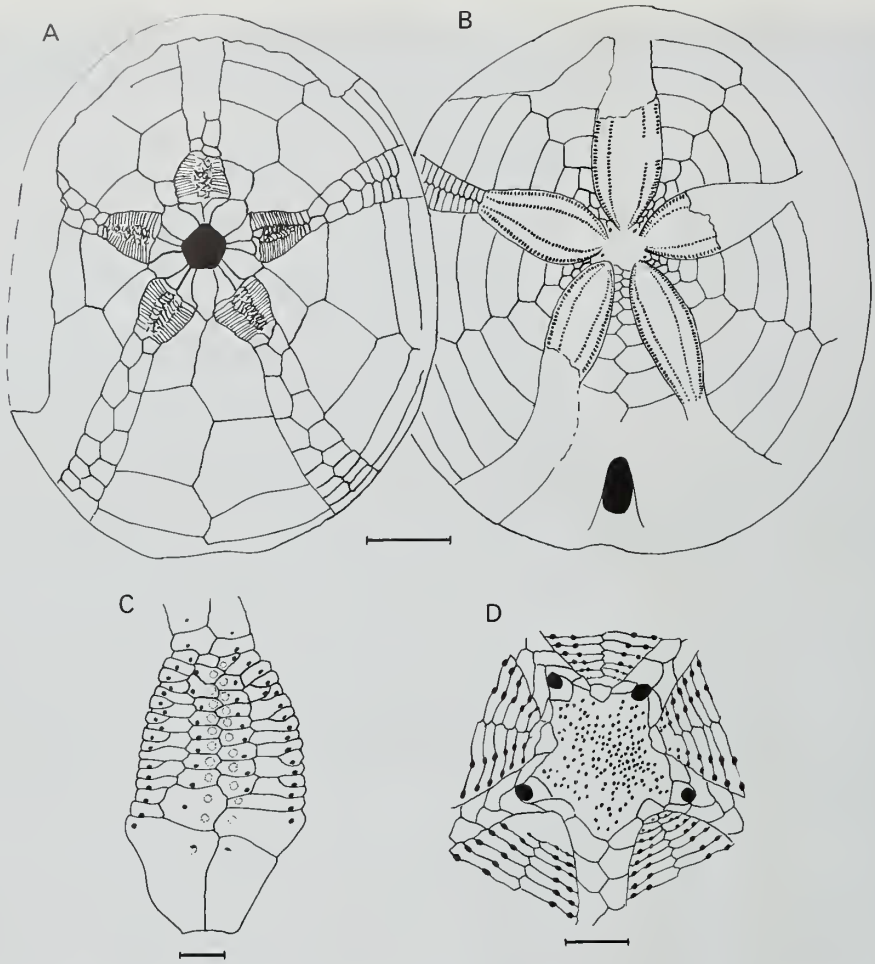


Fig. 68 Camera lucida drawings of plating in *Petalobrissus linguiformis* (Peron & Gauthier). **A**, oral surface, BMNH EE3344; **B**, apical surface, BMNH EE3345; **C**, oral phyllode, peristomial margin at base, BMNH EE3334; **D**, apical disc, BMNH EE3345. Scale bars: A, B = 5 mm; C, D = 1 mm.

Genus ***STIGMATOPYGUS*** d'Orbigny, 1856

Stigmatopygus pulchellus? sp. nov. Pl. 27, figs 1–8; Figs 69, 70

TYPES. Holotype BMNH EE4314, paratypes, BMNH EE3324–25, EE3329–30, EE3332–33, EE4312–13: all nine specimens were used for the biometric analysis given below in the description.

OTHER MATERIAL. In addition a further six specimens were collected.

OCCURRENCE. The species has been found only at Jebel Rawdah, section 2, at the following horizons: bed 14 (6); bed 19 (1); bed 21 (7); loose in scree, derived from beds 14–21 (1).

DESCRIPTION. Tests are elongate oval in outline, with a rounded anterior and a small posterior indentation (Pl. 28, figs 2–7). Tests range in length from 37 to 68 mm. Test width is 77–84% of test length (mean = 80%, SD = 1·9%, N = 9) and the widest point is slightly posterior of midlength. Test height is 41–56% of test length (mean = 47, SD = 4·9%, N = 9). The test has a depressed profile with the highest point coincidental with the apical disc and thus anterior of centre. There is a posterior notch marking the position of the periproct, and a small heel underneath the periproct in profile (Pl. 27, fig. 5).

The apical disc lies anterior of centre, some 32–40% of test length from the anterior border (mean = 37%, SD = 3·4%, N = 7). It appears to be tetrabasal, although the madrepores extend almost up to the start of the gonopores (Fig. 70D). There is no evidence for sexual dimorphism amongst the specimens to hand.

The petals are bowed, and are widest about one third of their distance from the apex (Pl. 27, fig. 7). The anterior petal has columns of equal length and the inner series of pores are almost straight. It is 22–27% of test length in length. The interporal zone is about twice as wide as the pore zone. Petal III is significantly longer than the rest. The petals in ambulacra II and IV are bowed and converge distally but remain open. The pore columns in the posterior petals are significantly different in length, with the inner series some 8–10 pore-pairs shorter than the outer column in larger specimens. These petals are also the narrowest.

All pores below the petals are single. Towards the peristome phyllodes are well-developed, and expand as an open

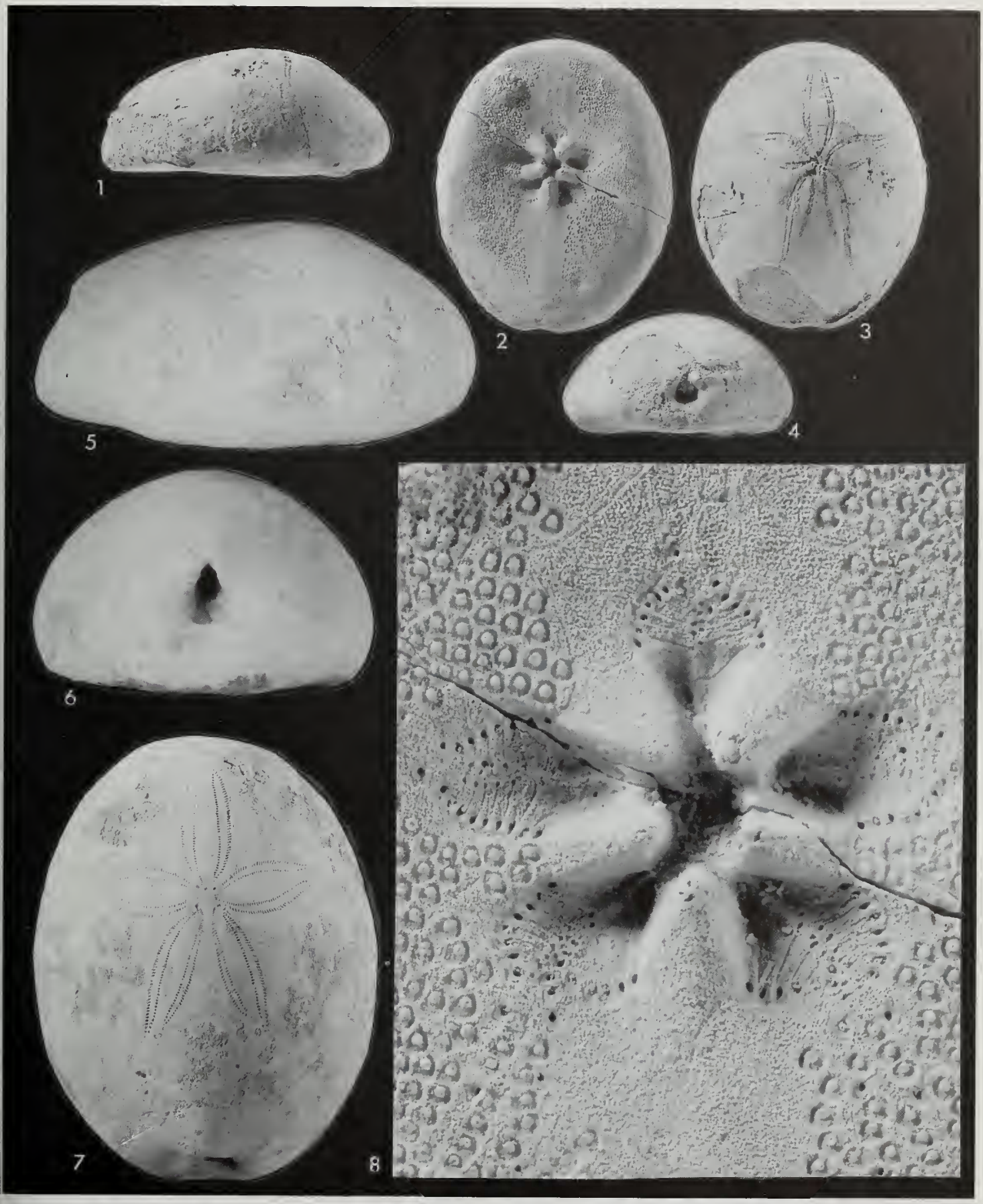


PLATE 27

Figs 1–8 *Stigmatopygus? pulchellus* sp. nov. **1–4**, **8**, BMNH EE4314, holotype; **1**, lateral, × 1; **2**, oral, × 1; **3**, apical, × 1; **4**, posterior, × 1; **8**, detail of peristomial region, × 5. Jebel Rawdah, section 2, bed 19. **5–7**, BMNH EE4313, paratype; **5**, lateral; **6**, posterior; **7**, apical; all × 2. Jebel Rawdah, section 2, bed 14.

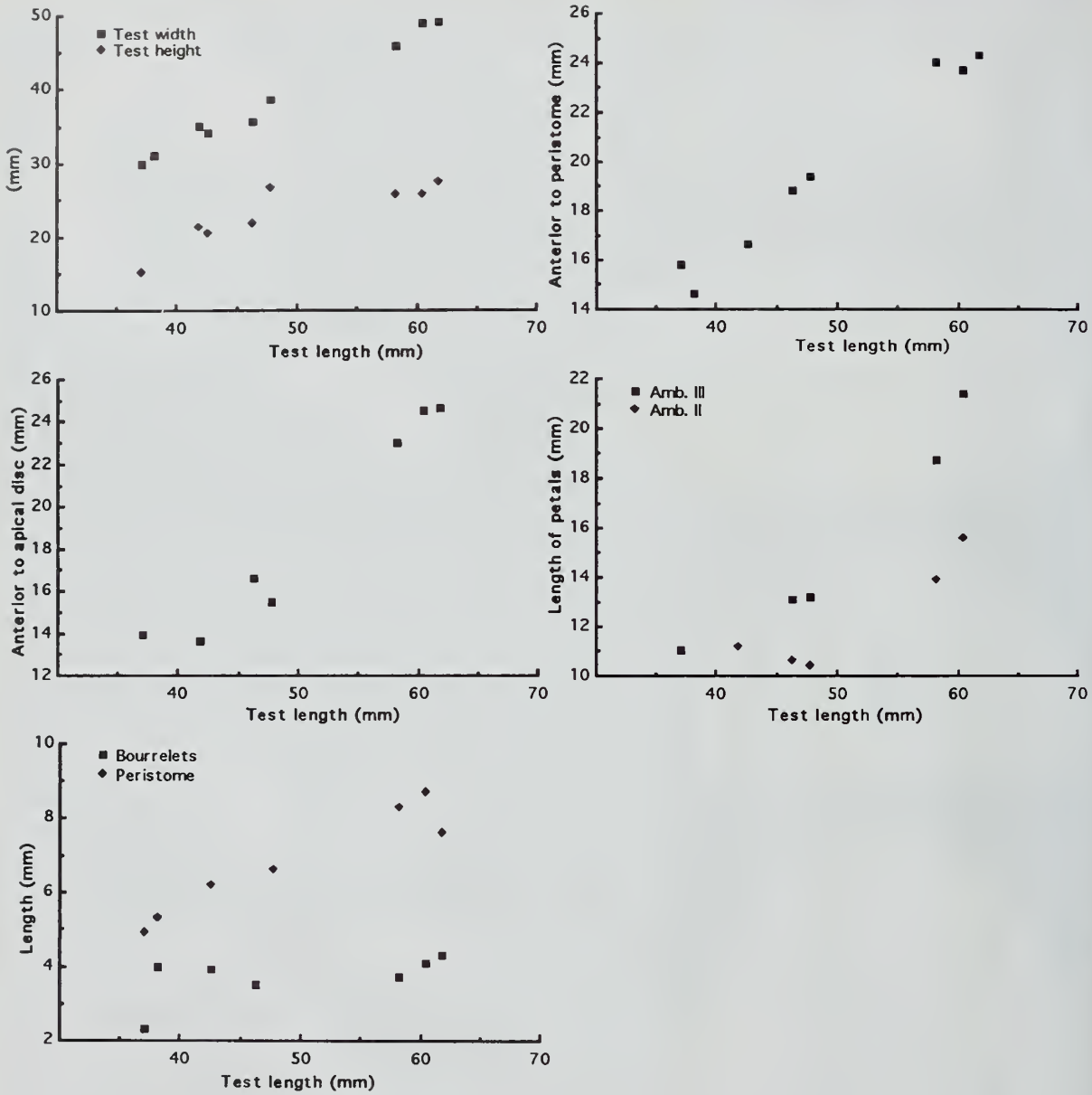


Fig. 69 Biometric data for *Stigmatopygus pulchellus* sp. nov.

'V' (Pl. 27, fig. 8). There are five or six pores in each series along the margin with an additional one, or rarely two inner pores at the distal end of the phyllodes (Fig. 70C). Usually there is only one occluded plate in each phyllode, all other plates extending from the adradial to the perradial suture. The first ambulacral plates are long and boot-shaped, with buccal pores that are much smaller than those composing the remainder of the phyllodes (Fig. 70C). Sphaeridial pits occur on each plate close to the midline, forming an alternating series, 4 or 5 per column. The phyllodes lie sunken relative to the surrounding test with buccal pores on the adoral walls of this depression, rather than in the peristomial well.

The peristome is pentagonal and either equilateral or slightly longer than wide (Pl. 27, fig. 8). Bourrelets are well developed, being straight-sided to weakly wedge-shaped in outline and projecting upwards strongly. They do not, however, project over the peristome.

The periproct is only just visible from above, being situated more or less posteriorly (Pl. 27, figs 6, 7). It is triangular in shape with an upper pinched portion and a broader, more rounded lower portion. It is typically slightly taller than broad. There is a subanal platform that extends as an invaginated floor to the periproct. There is a slight aboral lip to the periproct. It lies 21–34% above the base of the test (mean = 27%, SD = 5·5%, N = 7).

Tuberculation is fine and uniform aborally, slightly coarser orally. There is a very broad and well-developed naked zone running the length of the posterior interambulacrum. A smaller naked zone is also present anteriorly along the midline. These zones are covered in a very fine granulation

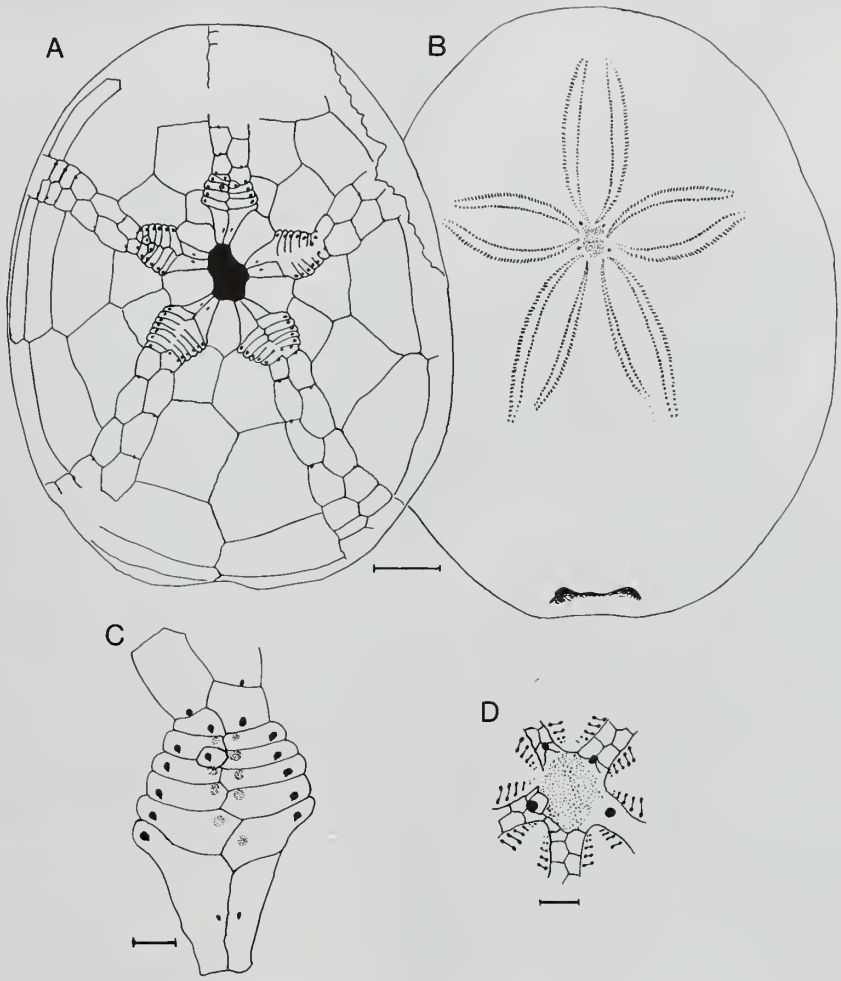


Fig. 70 Camera lucida drawings of plating in *Stigmatopygus pulchellus* sp. nov. **A**, oral surface, BMNH EE4312; **B**, apical surface, BMNH EE4314; **C**, phyllode plating, peristomial margin at base, BMNH EE4312; **D**, apical disc, BMNH EE3325. Scale bars: A, B = 5 mm; C, D = 1 mm.

but appear smooth to the naked eye.

REMARKS. This is a very distinct species, on account of its asymmetric posterior petals and keyhole-shaped periproct. Small forms resemble *Petalobrissus linguiformis* (Peron & Gauthier), but are easily distinguished from that species by their phyllode structure and periproct shape. *P. linguiformis* has a longitudinal periproct with a short parallel-sided anal sulcus, and also has much better developed phyllodes, with a separate series of inner occluded plates.

The new species undoubtedly comes closest to the type species of *Stigmatopygus*, *S. galeatus* d'Orbigny from the late Cretaceous of Angouleme, France. Both have a very similar test shape and periproct position and shape. Unfortunately, this species is very poorly known, the original description and figures being quite inadequate by today's standards. In particular its phyllode structure is unreported. Kier (1962) described the phyllode structure of another species *S. lamberti* Bessairie, from the Campanian of Madagascar, but this differs in being much wider and taller, with a much larger periproct. It also has better developed phyllodes, which are clearly bowed and comprise an outer series of some 12 pores and an inner series of 4 or 5 pores. I am therefore not certain that *S. lamberti* is truly congeneric with the type species *S. galeatus*. Only re-study of the type (apparently lost), or topotype material will solve the problem. If the phyllode structure of *S. galeatus* is similar to that of *S. pulchellus*, then *S. lamberti* should be transferred to a new genus. On the other hand, if *S. galeatus* proves to have a phyllode structure similar to that of *S. lamberti*, then *S. pulchellus* should be made the type of a new genus. Consequently, *S. pulchellus* can only tentatively be placed in the genus *Stigmatopygus*.

S. galeatus can be distinguished from *S. pulchellus* by the fact that its petals are illustrated as being of equal length.

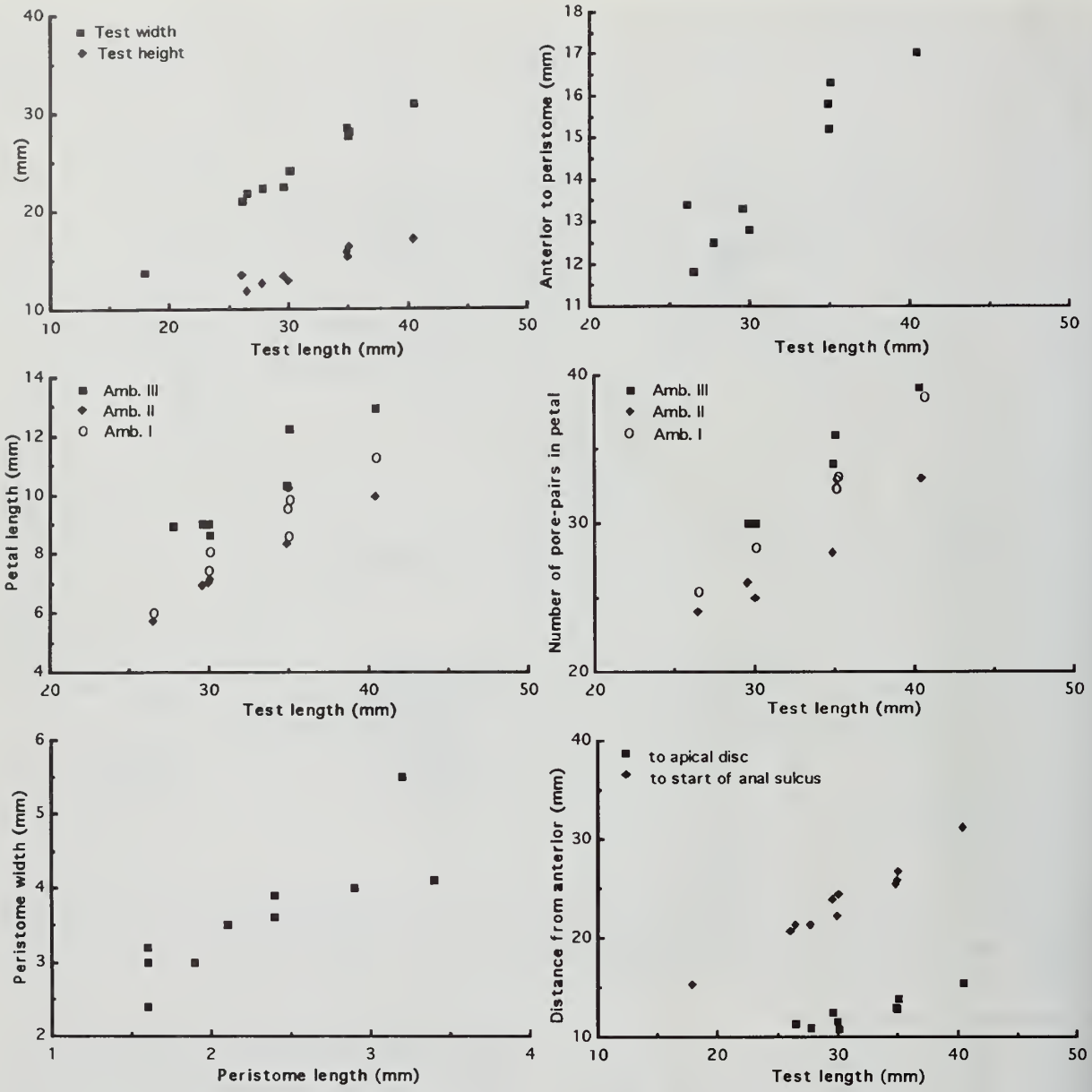


Fig. 71 Biometric data for *Nucleopygus magnus* sp. nov.

Genus *NUCLEOPYGUS* Agassiz, 1840

Nucleopygus magnus sp. nov. Pl. 28, figs 1–7; Figs 71, 72

TYPES. Holotype BMNH EE4339, paratypes, BMNH EE3340, EE3356, EE3358, EE3363, EE3365, EE3367–68, EE4327, EE4335–38

OTHER MATERIAL. An additional 29 specimens were collected. Biometric data was taken from the type series only.

OCCURRENCE. This species was found at the following localities and horizons:

Jebel Buhays, section 1: loose in scree, derived from the lowest few metres of the Simsima Formation (19).

Jebel Buhays, section 3: loose, derived from the lowest bed of the Simsima Formation (1).

Jebel Thanais: lowest 2 m of the Simsima Formation (4).

Jebel Rawdah, section 2: bed 14 (8); loose in scree (3).

Jebel Rawdah, section 4: bed 12 (1).

Jebel Faiyah, section 1b: bed 2 (1).

DIAGNOSIS. A very large, elongate *Nucleopygus* with a deep median depression on the oral surface. The periproct opens relatively close to the posterior border and there is only a short anal sulcus. The posterior petals end at a level slightly anterior to the start of the anal sulcus.

DESCRIPTION. Tests are subquadrate in outline, with a rounded anterior and a somewhat truncated posterior with a shallow anal notch (Pl. 28, figs 1, 4, 5). Test length ranges

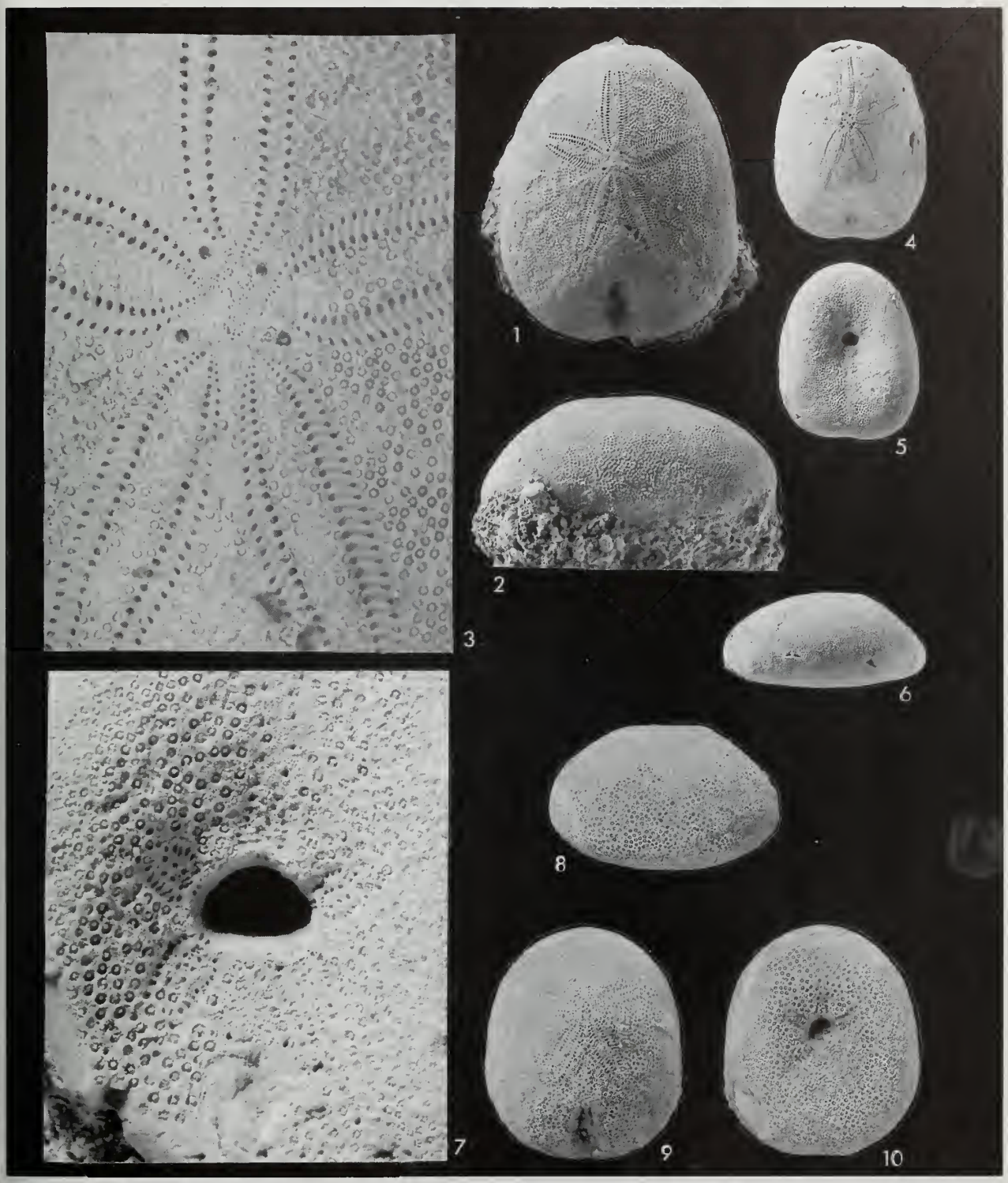


PLATE 28

Figs 1–7 *Nucleopygus magnus* sp. nov. **1–3**, BMNH EE4327, paratype; **1**, apical, × 2; **2**, lateral, × 2; **3**, detail of apical disc, × 4. Jebel Thanais, lowest 2 m of the Simsima Formation. **4–6**, BMNH EE4339, holotype; **4**, apical; **5**, oral; **6**, lateral; all × 1. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation. **7**, BMNH EE3367; detail of peristomial region, × 4. Jebel Buhays, section 2; loose in the scree derived from the lowest 3 m of the Simsima Formation.

Figs 8–10 *Nucleopygus iranicus* (Cotteau & Gauthier). Specimen in the Morgan Collection, Museum d'Histoire Naturelle, Paris; **8**, lateral; **9**, apical; **10**, oral; all × 2. Senonian, Poucht-e-Kouh, Iran.

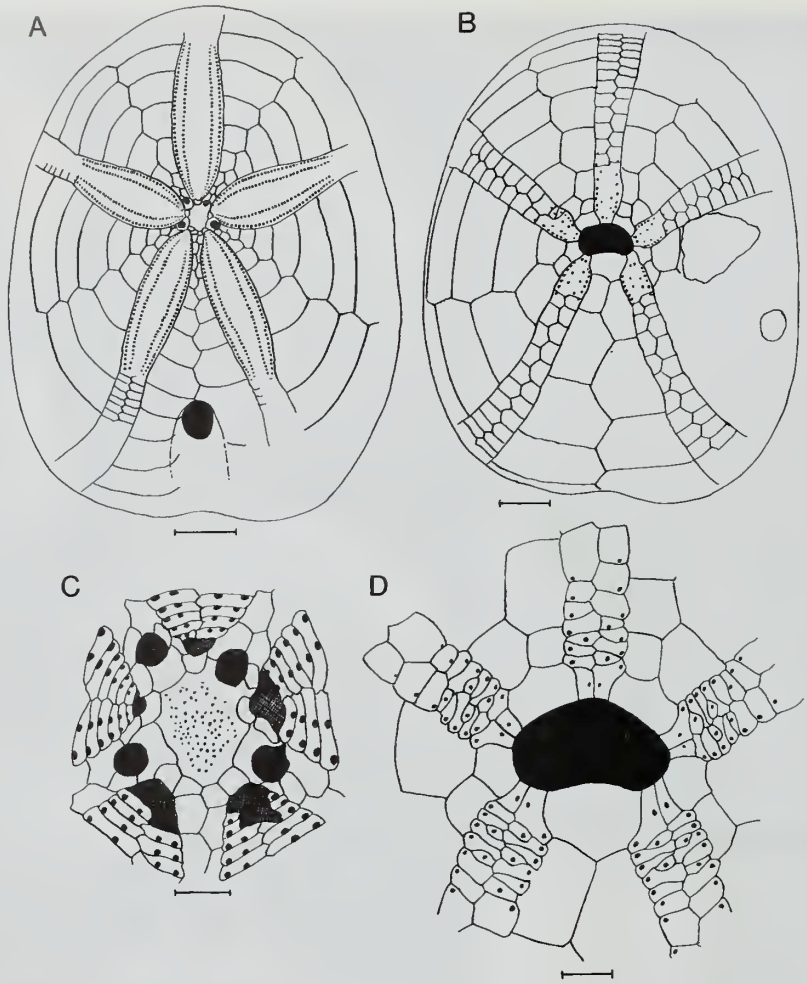


Fig. 72 Camera lucida drawings of plating in *Nucleopygus magnus* sp. nov. **A**, apical surface, BMNH EE4339; **B**, oral surface, BMNH EE4337; **C**, apical disc, BMNH EE4339; **D**, phyllode plating, BMNH EE4337. Scale bars: A, B = 5 mm; C, D = 1 mm.

from 18 mm to about 60 mm (estimated from a broken specimen). Test width is 76–82% of test length (mean = 79%, SD = 2%, N = 11), and the widest point on the test is about two thirds of the distance back from the anterior. The test has a low profile, with test height 42–51% of test length (mean = 39%, SD = 3%, N = 9). It is rounded towards the anterior but obliquely truncated towards the posterior (Pl. 27, figs 2, 6). The ambitus is rounded, but relatively low. The oral surface has a marked median depression and the peristome is sunken (Pl. 28, fig. 5).

The apical disc lies 36–43% of the test length from the anterior border (mean = 39%, SD = 1%, N = 9). It is tetrabasal with large gonopores projecting into the interambulacra (Fig. 72C). Ocular plates are small and U-shaped. The small genital plates are separated from one another by ocular plates.

Petals are open and subparallel to very slightly bowed (lateral and posterior pairs) (Pl. 28, figs 1, 4; Fig. 72A). Pores are both approximately circular and are joined by a well-marked furrow (Pl. 28, fig. 3). The interporal zone is approximately 1·5 times as wide as a pore-zone. The anterior petal is the longest, but is only slightly longer than the posterior petals. It has 30 pore-pairs in a column at 30 mm test length, rising to 40 at 40 mm test length. The posterior petals end slightly in front of the anal sulcus.

All pores are single below the petals. Phyllodes are hardly expanded adorally (Pl. 28, fig. 7; Fig. 72D). There are buccal pores at the rim of the peristome, situated on relatively short and squat first ambulacral plates. The phyllodes have both an outer and an inner series of pores, although the two series are not well separated (Fig. 72D). There are six pores per column in the outer series in ambulacrum III with 7 or 8 in the other ambulacra, and 1 or 2 pores in the inner series of ambulacrum III with 2 or 3 in other ambulacra. Every third ambulacral plate is occluded, but the occluded plates do not form a continuous inner series. The phyllodes are not depressed relative to the surrounding test. There are no bourrelets, but the walls to the peristome are covered with fine, dense tubercules. The posterior interambulacrum differs from other interambulacra in that it does not turn sharply in towards the peristome, but instead forms a sloping shelf into the opening.

The peristome is pentagonal in outline, approximately 1·6 times as wide as long. It lies 38–42% of the test length from the anterior border (mean = 40%, SD = 1%, N = 10).

The periproct is tall and narrow and has a width approximately 40% of its height. It opens into a narrow, parallel-

sided anal sulcus that slopes posteriorly. The periproct opens 73–85% of test length from the anterior border (mean = 78%, SD = 4%, N = 11).

The upper surface is covered in fine, slightly sunken tubercles. Adorally tubercles are coarser but are still sunken. There is a narrow, zig-zagged granular zone in the posterior interambulacrum that follows the interradial suture and tapers out before reaching the pesterior border (Pl. 27, fig. 7). It is never more than about 78% of the test width at its widest.

REMARKS. Few other species of *Nucleopygus* come anywhere near the size of *N. magnus*. Both *N. iranicus* (Cotteau & Gauthier) (Pl. 28, figs 8–10), from the late Cretaceous of southern Iran, and *N. pullatus* Stolizcka, from the Maastrichtian of southern India are much smaller species, reaching little more than 14 mm in test length. Furthermore, they are squatter. *N. geayi* (Cottreau), from the Maastrichtian of Madagascar, is even smaller, never being reported larger than 8 mm test length. Similarly, the European species *N. coravium* and *N. scrobiculatus* are equally small forms.

Only in the late Cretaceous of North Africa do any *Nucleopygus* approach the size of *N. magnus*. *N. inaequalis* (Peron & Gauthier) resembles *N. magnus* in shape but its posterior petals extend posteriorly beyond the start of the anal sulcus. *N. meslei* (Peron & Gauthier), from the Campanian, is probably the closest. *N. meslei* reaches 30 mm in test length, but differs from *N. magnus* in having a more anterior apical disc, a longer anal sulcus and more petaloid ambulacra. It is also less markedly depressed along the midline on the oral surface.

Family **ECHINOLAMPADIDAE** Gray, 1851
Genus ***ARNAUDASTER*** Lambert, 1918

REMARKS. Until now there has only been one species assigned to this genus, *A. gauthieri* Lambert, from the Cenomanian of France (Aquitaine). Kier (1962: 105) noted that *Arnaudaster* might best be considered a synonym of *Parapygus*, as it differs only in having a more cylindrical shape and more unequal poriferous zones in the same petal. The discovery of a Maastrichtian species very close in form to *A. gauthieri* supports the maintenance of *Arnaudaster* as a separate genus. *Pseudocatopygus longior* Cotteau & Gauthier, from the late Cretaceous of Iran, also has unequal columns in its petals and may belong to *Arnaudaster*. However, Kier (1962) placed *Pseudocatopygus* as a synonym of *Parapygus*.

Arnaudaster cylindriformis sp. nov. Pl. 25, figs 11, 12; Pl. 29, figs 1–9; Figs 73–75

TYPES. The holotype is BMNH EE4334, paratypes are BMNH EE4324, EE4331–33, EE3378–81.

OTHER MATERIAL. Three poorly preserved specimens, BMNH EE3374–76. BMNH EE3373 may also belong here, but only a fragment of the upper surface is preserved and this apparently shows equally developed columns of pore-pairs in ambulacrum petal V.

OCCURRENCE. This species was found at the following localities along the western margin of the Oman Mountains:
Jebel Buhays, section 1: top of bed 1 (1); loose in the scree, derived from the lowest few metres of the Simsima Formation (6).
Jebel Rawdah, section 2: bed 14 (1); loose at the level of bed 19 (2); loose in scree, derived from beds 14–21 (2); bed 21 (1); bed 26 (1).
Jebel Rawdah, section 3: bed 9 (1); loose near top of section (1).

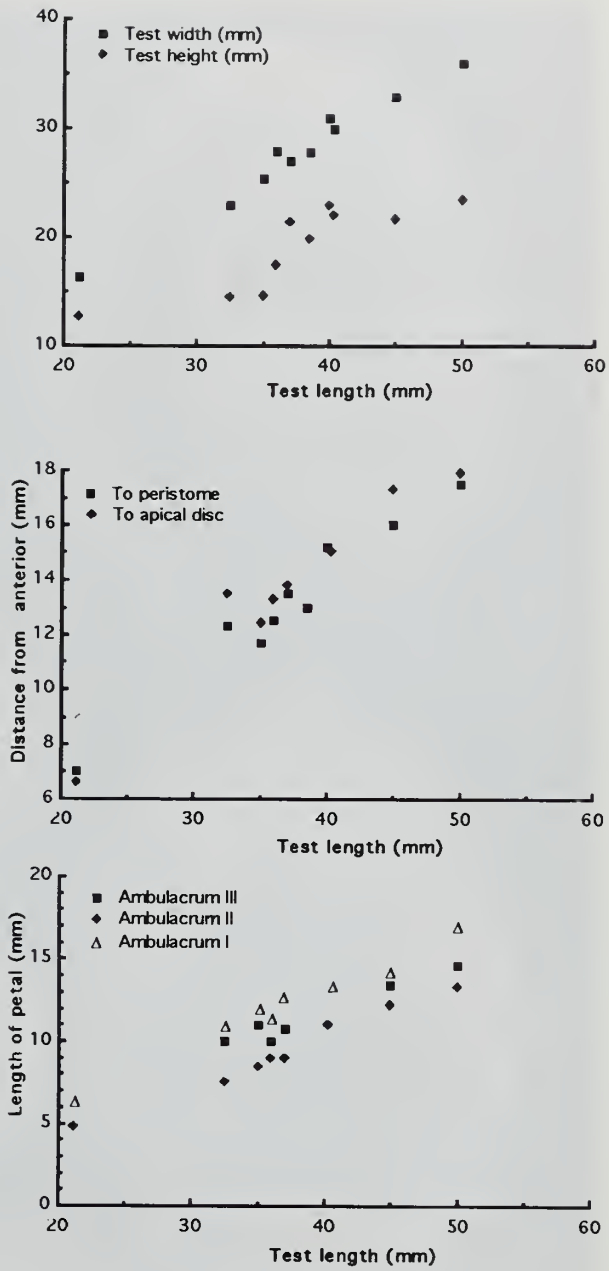


Fig. 73 Biometric data for *Arnaudaster cylindriformis* sp. nov.

DIAGNOSIS. An *Arnaudaster* with a wide, pentagonal peristome with weak bourrelets and approximately four pores in the inner series of phyllodes in each half ambulacrum.

DESCRIPTION. Tests range from 21 to approximately 50 mm in length, although many specimens are lacking the very

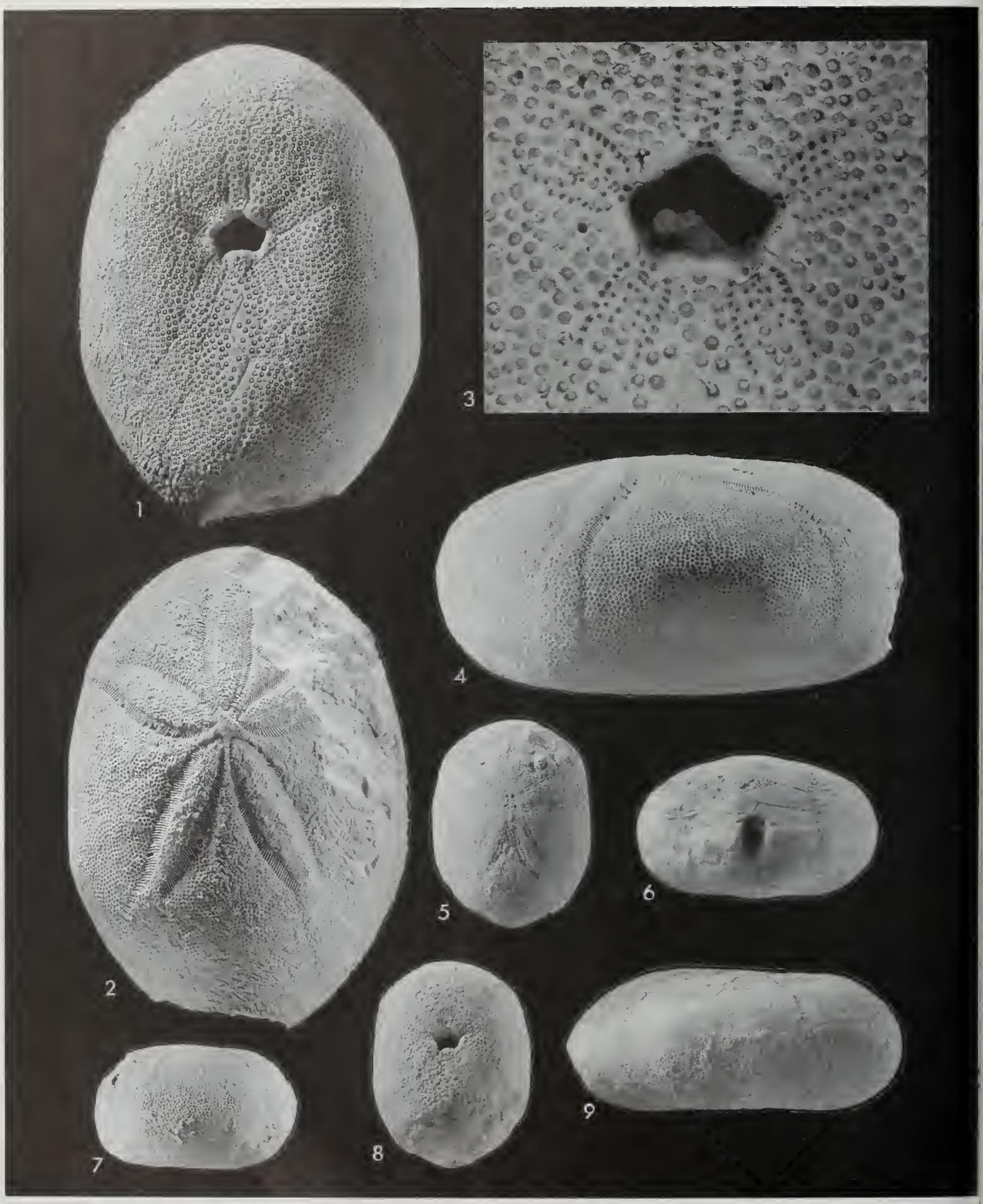


PLATE 29

Figs 1–9 *Arnaudaster cylindriformis* sp. nov. **1–4**, BMNH EE4334, holotype; **1**, oral, × 2; **2**, apical, × 2; **3**, detail of peristomial region, × 4, **4**, lateral, × 2. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation. **5, 7, 8,** BMNH EE4323; **5**, apical; **7**, lateral; **8**, oral; all × 2. Jebel Rawdah, section 2, bed 21. **6, 9,** BMNH EE4324 (depressed variety); **6**, posterior; **9**, lateral; both × 2 (see also Pl. 25, Figs 11, 12). Jebel Rawdah, section 2, bed 14.

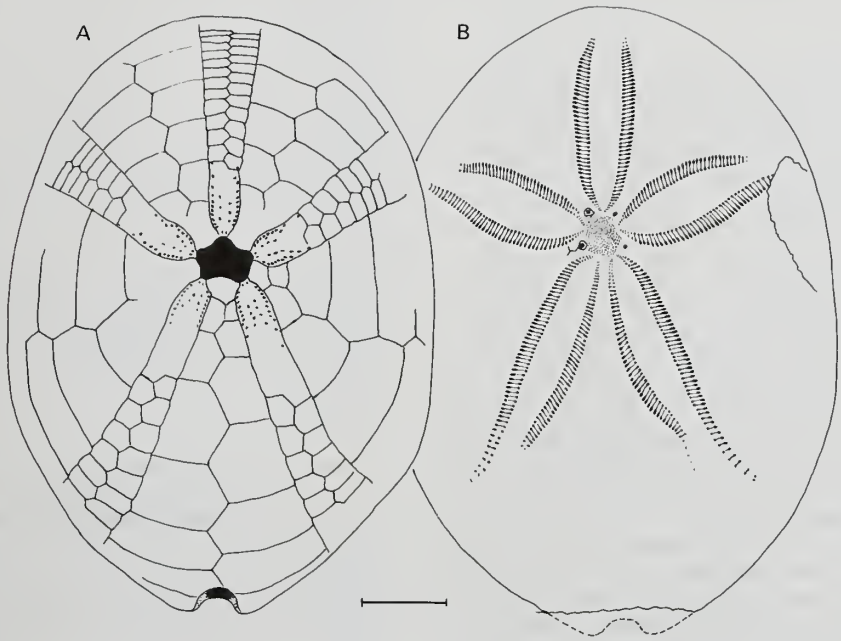


Fig. 74 Camera lucida drawing of plating in *Arnaudaster cylindriformis* sp. nov. **A**, oral surface, BMNH EE4324; **B**, apical surface, BMNH EE4333. Scale bar = 5 mm.

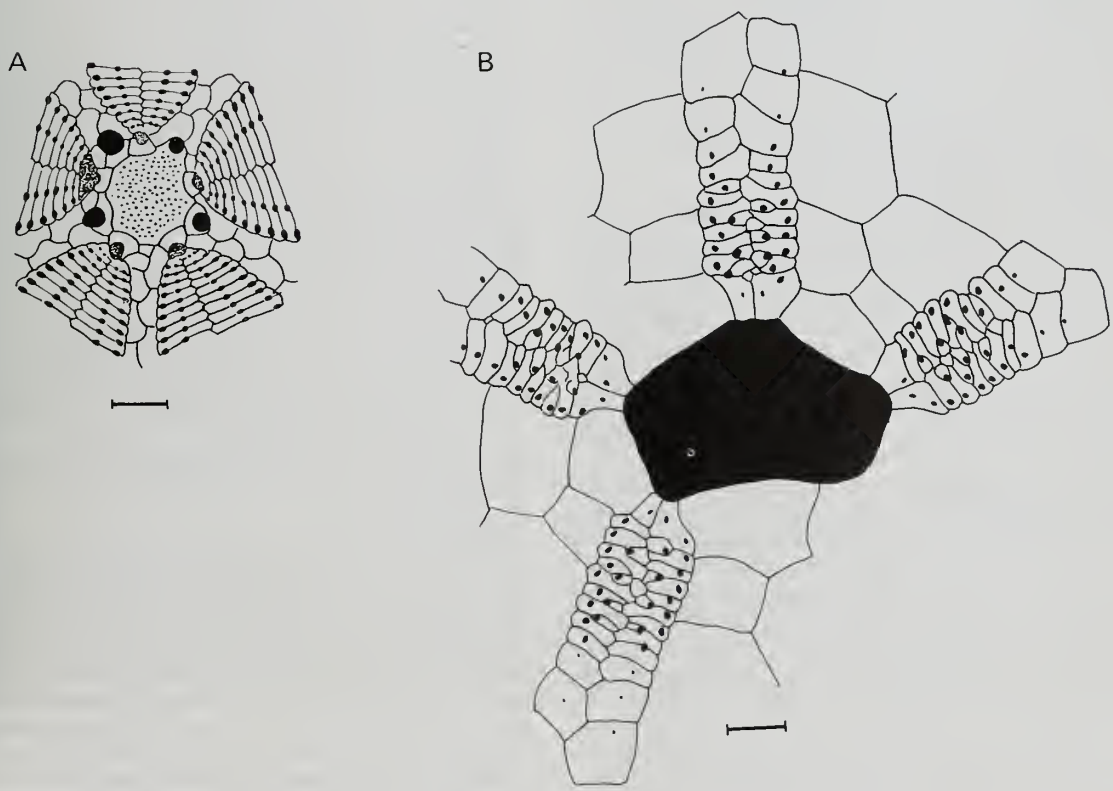


Fig. 75 Camera lucida drawings of plating in *Arnaudaster cylindriformis* sp. nov. **A**, apical disc, BMNH EE3379; **B**, phyllode plating, BMNH EE4324. Scale bars = 1 mm.

posterior end of the test. Tests are ovoid in outline with a rounded anterior and a very weakly pointed posterior (Pl. 25, figs 11, 12; Pl. 29, figs 1, 8). Test width is 71–78% of test length (mean = 74%, SD = 2·5%, N = 10), with the widest point on the test approximately two thirds of the distance from the anterior and well behind the level of the apical disc. Test height is 41–60% of the length (mean = 51%, SD = 6·1%, N = 10). In profile the upper surface is broad and almost flat, uniformly rounded at the anterior, but undercut at the posterior (Pl. 29, figs 4, 7, 9). The oral surface is flat or very slightly sunken towards the peristome, while the ambitus is smoothly rounded.

The apical disc lies well anterior of centre, some 31–41% of test length from the anterior border (mean = 37%, SD = 2·9%, N = 8). Plating is tetrabasal, although genital plate 2 is enormously enlarged in comparison to the other genital plates and occupies the centre of the disc (Fig. 74A). The entire madreporic plate is covered in dense, fine perforations. Other genital plates are very small and are dominated by the gonopores. There may be sexual dimorphism in the size of gonopore openings. Ocular plates are small, approximately the same size as the genital plates.

Ambulacra are petaloid with the interporal zone slightly inflated. The anterior and two posterior petals are similar in size, but the lateral petals are shorter. Petals are broad, lanceolate with more or less parallel columns of pore-pairs at the distal tip (Pl. 29, fig. 2; Fig. 74B). They extend about 80% of the distance to the ambitus. Pore-pairs are conjugate. The anterior petal has columns of equal length, with 41 pore-pairs in a column at 32 mm test length, rising to 57 at 50 mm test length. The anterior column of pore-pairs in the lateral petals is shorter than the posterior column by about five pore-pairs (Fig. 74B). Distally they are slightly narrower, but remain broadly open. The posterior petals also have unequally developed columns of pore-pairs, with the posterior column shorter than the anterior column by seven or so pore-pairs. They extend approximately 70% of the distance to the ambitus and remain broadly open distally.

Below the petals pores are single. Phyllodes are not strongly developed and phyllode plating is best seen in BMNH EE3379. Pores of the outer series become enlarged close to the peristome, but the rows of pores do not bow out (Fig. 75B). There are only eight or nine pores forming the outer series in one half ambulacrum. There are three or four pores forming an inner series in each half ambulacrum. Each inner series pore is found on an occluded plate (Fig. 75B). There are small but obvious buccal pores which are not separated from the other pores of the phyllode but which open right at the peristomial rim.

The first interambulacral plates are short and wide and are slightly swollen to form a weak floscelle (Pl. 29, fig. 3; Fig. 75B). The peristome is pentagonal, approximately twice as wide as long, and with well-developed vertical walls.

The periproct is small and transversely oval, with a width approximately 50–70% of its height. It lies at approximately mid-height on the posterior face, but is angled slightly downwards so that it is just visible from the oral surface and not from the adapical surface (Pl. 29, figs 5, 8). Because the posterior of the test is slightly drawn out, the periproctal region is often damaged. The base of the periproct lies between about 30 and 40% of the test height above the base. Tubercles are small, sunken and densely crowded over the whole surface.

Remarks. This species comes very close to the type species *A. gauthieri* in almost every respect. Both have a very similar, cylindrical test, anterior apical disc and strongly unequal columns of pores in both lateral and posterior petals (the same columns that are asymmetric). The only difference of significance appears to be in the development of phyllodes. In *A. gauthieri* the inner series of pores is rather poorly developed and not well separated from the outer series. In *A. cylindriformis* the inner series pores are somewhat more numerous and form a distinct series. However, this is a minor difference, and there is very little else to separate the two forms.

The species also resembles *Parapygus inflatus* Cotteau & Gauthier in its overall shape and appearance. However, Cotteau & Gauthier catagorically state (1895: 55) that the columns of pore-pairs in the petals of the species are equally developed.

Order **HOLASTEROIDA** Durham & Melville, 1957
Family **HOLASTERIDAE** Pictet, 1857
Genus ***HEMIPNEUSTES*** Agassiz, 1836

Diagnosis. Heart-shaped holasteroids showing pronounced petal asymmetry, with the posterior column of pores well developed and anterior column rudimentary. Periproct subambital and clearly visible in oral view because of the distinct posterior notch. The madrepores extend over all genital plates as well as the anterior three ocular plates. Plastron plates wedge-shaped, each just reaching the opposite adradial suture and thus biserially arranged.

Occurrence. Late Campanian and Maastrichtian, Europe, North Africa and the Middle East.

Remarks. *Hemipneustes* is very close in appearance to *Cardiaster*. Both have a cordiform test with a deep, well-defined anterior sulcus which has enlarged primary tubercles along its border. Both genera also have a similar style of plastron plating, composed of a short, broad labral plate followed by up to five wedge-shaped plates which more or less occupy the full width of the plastron (eg. Ernst 1972, text-fig. 20). Finally, both have rather similar petals, with the anterior column greatly reduced in comparison to the posterior column. The primary difference between *Cardiaster* and *Hemipneustes* lies in the fact that *Hemipneustes* has little more than rudimentary pore-pairs in the anterior columns of its petals, whereas *Cardiaster* has small but distinctly conjugate pore-pairs in these anterior columns. Furthermore, madrepores are more extensively developed in *Hemipneustes*, extending beyond genital plate 2 to cover genital plate 3 and ocular plates II, III and IV.

Many species names have been erected in the past, mostly based on relatively few specimens and often on rather poorly preserved material. From Noetling (1897) onwards workers have relied on two simple biometric indicators to distinguish species of this genus; width/length and height/length ratios (see for example Devries 1967; Aziz & Badve 1990). However, not only do these ratios vary ontogenetically and thus vary according to absolute test size, but they have also rarely been applied rigorously using large populations.

There are three species found amongst the material collected from the Oman Mountains. These appear to have some stratigraphic value. The lowest forms found at Jebel Rawdah belong to *H. persicus* var. *sardanyolae* Vidal, and

are found in the basal sandy facies. These have the broad shallow anterior sulcus characteristic of the *H. delettrei* complex, a group restricted to the late Campanian of Tunisia and Algeria (Zhagbib-Turki 1987). Above this, or possibly partially overlapping, *H. arabicus* is found. This species is similar in profile and in the positioning of its apical disc, but has a much narrower, deeper and more sharply defined anterior sulcus. The first elevated *Hemipneustes* forms, belonging to *H. compressus,* appear in bed 14, having more uniformly rounded profiles. However, by the time bed 21 is reached, *H. compressus* has a much more quadrate profile with strongly pinched ridges to the frontal groove. Finally, by bed 26 some *H. compressus* appear that are very elevated and which have developed a strong slope towards the posterior similar to the late Maastrichtian *H. striatoradiatus*.

In trying to identify the Oman/United Arab Emirates species, a number of other species have been examined and the following are accepted as valid:

Hemipneustes delettrei Peron & Gauthier (Pl. 30, figs 9, 10), late Campanian of Algeria. Rounded in outline and variable in profile, from highly inflated (*H. africanus* form) to depressed (*H. delettrei* form). w/l = 0·89–0·95 (mean = 0·91): h/l = 0·58–0·79 (mean =0·70) [size range 73–98 mm]. Distinguished from all other species by the large, broad anterior ambulacral sulcus; about twice as broad as in any other species.

Hemipneustes striatoradiatus (Leske) (Pl. 30, figs 7, 8; Fig. 78C), Upper Maastrichtian of the Netherlands. Rounded in outline with a very narrow and shallow anteal sulcus. Variable in profile from flat-topped to distinctly raised anterior to the apical disc. Sides rather vertical giving quadrate cross-section. Apical disc anterior of centre. w/l = 0·87–0·97, mean = 0·91: h/l = 0·61–0·80, mean 0·69 [Size range 50–100 mm]. Distinguished from other species by (i) its narrow, shallow anteal sulcus, (ii) rounded outline and (iii) quadrate lateral cross-section.

Hemipneustes pyrenaicus Hebert (Pl. 30, figs 5, 6) – closest to *H. compressus* in having a short narrow frontal groove with a strong vertical component, anterior apical disc, and quadrate profile. It differs in having a flat apical surface and in lacking adapical pinched ridges to the anterior sulcus.

H. persicus Cotteau & Gauthier (Pl. 31, figs 1–7; Pl. 32, figs 1–4; described below).

H. compressus Noetling (Pl. 31, figs 8–11; described below).

H. arabicus Ali (Pl. 30, figs 1–4; described below).

In addition the following species are treated as synonyms or rejected names, or are based on inadequate material:

H. minor Peron & Gauthier, Upper Senonian of Iran (a small *H. persicus* Peron & Gauthier).

H. oculatus Cotteau, Maastrichtian of Ciply, Belgium. This appears to be a large variety of *H. striatoradiatus*, somewhat crushed but with a deeper frontal groove as illustrated by Cotteau. The specimens referred to under this name by van der Ham (1989) are simply rather tall and posteriorly inclined *H. striatoradiatus*.

H. arnaudi Cotteau 1892, Upper Senonian of Dordogne. This is very like high forms of *H. compressus* in having an elevated keel to the ambulacrum. It has too wide an anterior sulcus to be a *H. striatoradiatus*. Treat as a probable synonym.

H. indicus Aziz & Badve 1990; Maastrichtian of S India, is identical in profile to *H. arnaudi* but larger. Its deep frontal groove and anterior apical disc makes it part of the *compressus* group.

H. sardanyolae Vidal 1921, Campanian of Spain, is treated here as a shallow grooved variety of *H. persicus*.

H. nicklesi Vidal 1921, Campanian of Spain, is a *Hemipneustes* sp. based on crushed and badly preserved specimens that are basically indeterminate. It is probably a synonym of *H. persicus* var. *sardanyolae* Vidal.

Spatangoides martelli Checchia-Rispoli, Maastrichtian of Libya. Here synonymized with *H. compressus* Noetling.

Spatangoides tripolitanus Checchia-Rispoli, Maastrichtian of Libya, is clearly a species of *Opisopneustes*. Its primary adapical interambulacral tubercles are well developed and it represents a valid species, differing from *O. cossoni* in having a vertically positioned periproct.

Spatangoides aichinoi Checchia-Rispoli, Maastrichtian of Libya. Here synonymized with *H. persicus*.

Hemipneustes batheri Lambert [=*H. leymeriei* Noetling]. This is probably a variety of *H. persicus*, having the posterior apical disc and oval outline with shallow and open anterior sulcus, but it is unusually tall.

H. noetlingi Lambert was erected as a replacement name for *H. pyrenaicus* of Noetling, from the Maastrichtian of Baluchistan. However, like Devries (1967), I can find no significant difference between Noetling's specimens and the type material of *H. pyrenaicus* and treat *H. noetlingi* as a junior synonym.

Hemipneustes leymeriei Hebert has the very narrow and shallow groove and circular outline of a *H. striatoradiatus*. Topotype material from Gansec, southern France, confirms this.

Spatangoides tripolitanus Checchia-Rispoli is a species of *Opisopneustes*.

Hemipneustes compressus Noetling, 1897 Pl. 31, figs 8–11; Figs 76, 77, 78A

1897 *Hemipneustes compressus* Noetling: 34, pl. 7, figs 3, 4, pl. 8, figs 1, 2.

1931 *Spatangoides Martellii* Checchia-Rispoli: 7, pl. 1, figs 1–3.

1967 *Hemipneustes compressus* Noetling; Devries: 188, pl. 6, figs 31–33.

TYPES. The syntypes are the four specimens illustrated by Noetling and presumably in the Geological Survey of India collections.

MATERIAL STUDIED. Thirty specimens were collected. Biometric data was taken from the following 16 specimens: BMNH EE3744–45, EE3748, EE4070–71, EE4073–74, EE4076, EE4078–82, EE5022–24.

OCCURRENCE. Maastrichtian of Libya, Oman and Baluchistan. In the western Oman Mountains it occurs at the following levels:

Jebel Rawdah, section 2: bed 14 (2); bed 15 (2); bed 19 (1); beds 20/21 (17); bed 22 (1); bed 26 (2 specimens plus fragments); bed 27 (2).

Jebel Rawdah, section 3: beds 9/10 (1).

Jebel Rawdah, section 4: loose, towards top of section (1).

DIAGNOSIS. Test rather more elongate than in other species, typically flat-topped in side-view and arched in cross-section.

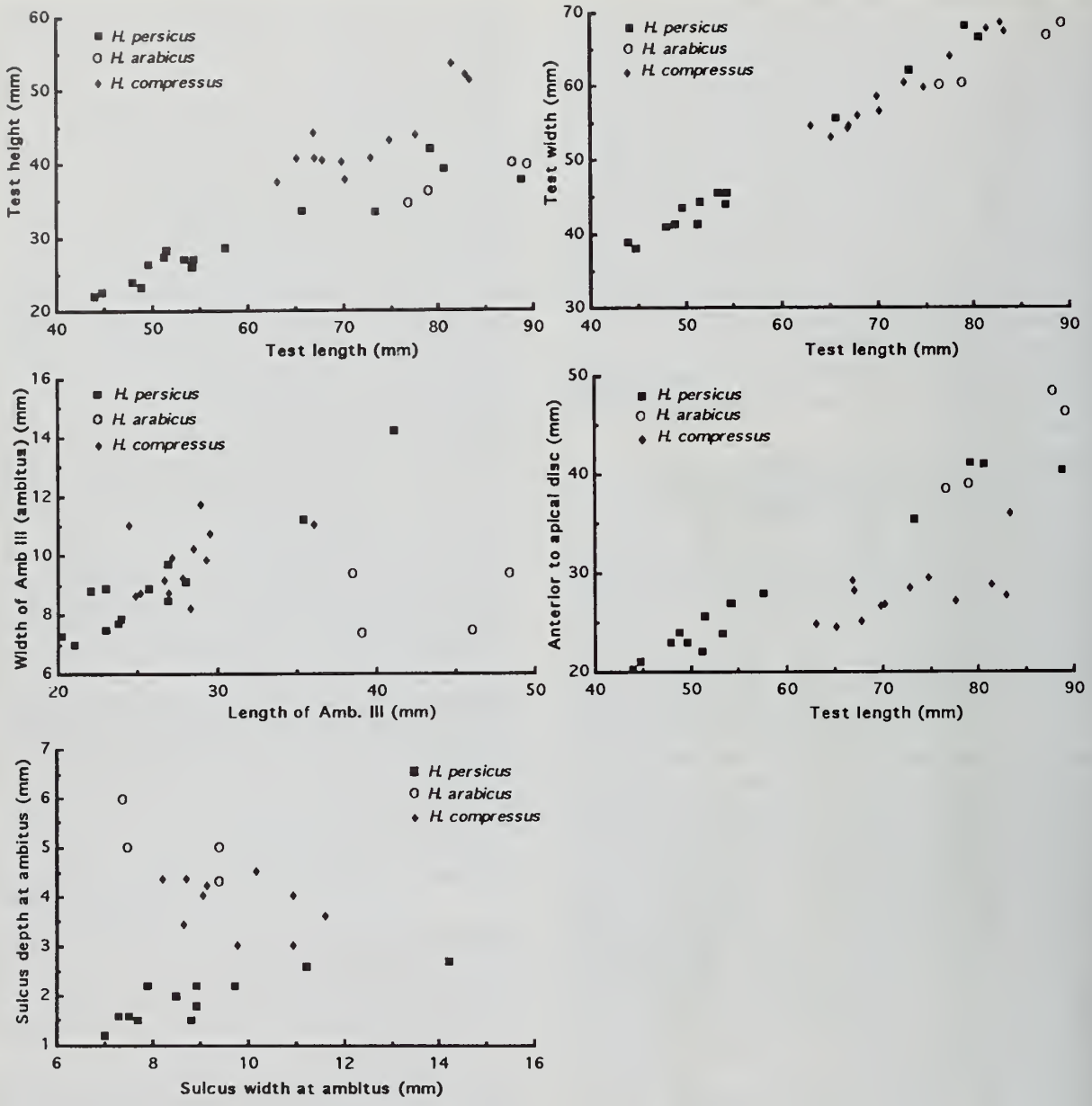


Fig. 76 Biometric data for species of *Hemipneustes*.

w/l = 80–87% of length, mean = 83%; height 54–67% of length, mean = 60% (size range 63–83 mm). Frontal groove narrow but moderately deep at the anterior; typically slightly keeled. Apical disc lies well towards the anterior (distance between anterior and apical disc = 34–44% of length: mean = 39%) and is pinched up. Distinguished from other species by (i) its anterior apical disc, (ii) the deep anterior groove which is relatively short and geniculate with a strong vertical component, (iii) being more subquadrate outline, typically inclined from the apical disc posteriorly.

DESCRIPTION. Tests range in length from 63 to 83 mm in length and from 53 to 69 mm in width (width = 80–87% of length; mean = 83%, SD = 1·8%, N = 13). In outline the test is cordate with a sharp, deep anterior sulcus, and a truncated and even slightly indented posterior (Pl. 31, figs 8, 9). The widest point on the test lies approximately mid-length. Test height is variable, ranging from 38 to 54 mm (height = 54–66% of test length: mean = 60%, SD = 3·7%, N = 13). In side view the upper surface varies from almost flat to strongly vaulted, with the tallest point on the test lying immediately anterior of the apical disc (Pl. 31, fig. 11). The test slopes towards the posterior which is truncated. Anterior to the apical disc the test curves uniformly to become almost vertical. There is a sharp curve from the anterior to the more or less flat base (Pl. 31, fig. 11). In anterior profile the test appears vaulted with rounded sides sloping up to the crest. The anterior sulcus becomes slightly pinched towards the base and its edges are sharply delimited (Pl. 31, figs 10, 11).

PLATE 30

Figs 1–4 *Hemipneustes arabicus* Ali. BMNH EE5027; **1**, oral; **2**, apical; **3**, anterior; **4**, lateral; all × 1. Jebel Rawdah, section 1, bed 4.

Figs 5, 6 *Hemipneustes pyrenaicus* Hebert. Specimen in the Museum d'Histoire Naturelle, Paris; Maastrichtian of Montbéraud, Haute Garonne, France. **5**, apical; **6**, lateral; both × 1.

Figs 7, 8 *Hemipneustes striatoradiatus* (Leske). BMNH 75822; **7**, apical; **8**, lateral; both × 1. Maastrichtian of Maastricht, The Netherlands.

Figs 9, 10 *Hemipneustes delettrei africanus* Peron & Gauthier. BMNH E3654; **9**, apical; **10**, lateral; both × 0·75. Upper Campanian of Ain Joutu, Algeria.

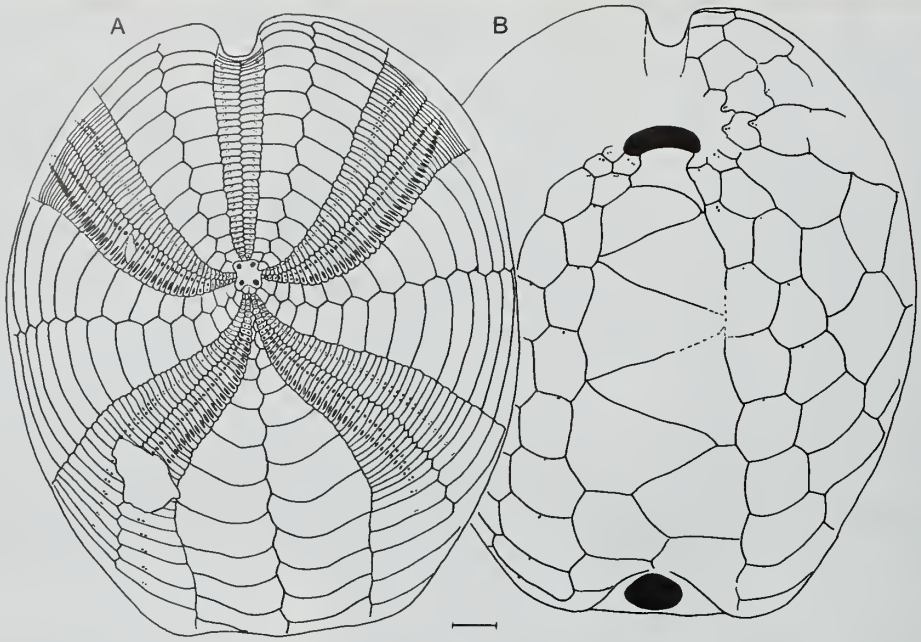


Fig. 77 Camera lucida drawings of plating in *Hemipneustes compressus* (Noetling), BMNH EE3745. **A,** apical surface; **B,** oral surface. Scale bar = 5 mm.

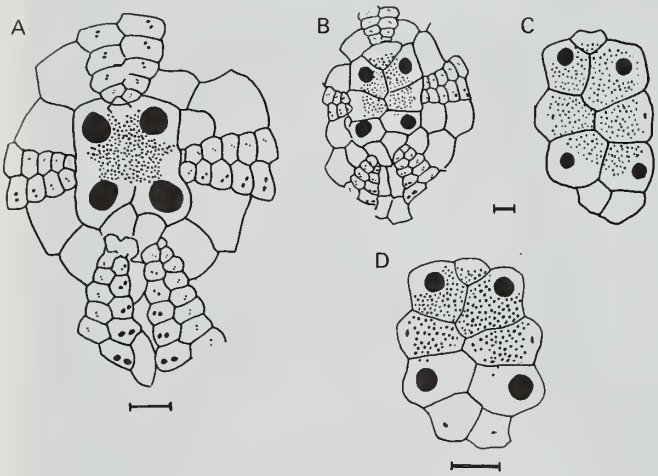


Fig. 78 Camera lucida drawings of apical disc plating in species of *Hemipneustes*. **A,** *H. compressus* (Noetling), BMNH EE3745; **B,** *H. arabicus*, BMNH EE5027; **C,** *H. striatoradiatus* (Leske), BMNH 38630; **D,** *H. persicus* Cotteau & Gauthier, BMNH EE3747. Scale bars = 1 mm.

The apical disc lies at or slightly in front of mid-length (distance to the anterior border = 34–44% of test length: mean = 39%, SD = 3·1%, N = 13). It is elongate with 4 gonopores occupying most of the area of the genital plates (Fig. 78A). The anterior pair of genital plates are separated from the posterior pair by the lateral ocular plates. Madrepores extend across genital plates 2 and 3, as well as ocular plates II, III and IV, even extending into the wall of the gonopores in some instances. The two posterior ocular plates are slightly larger and abut each other.

The anterior ambulacrum is non-petalloid. It is almost flush at the apex, becomes slightly depressed towards the anterior and then forms a deep vertical sulcus close to the anterior (Pl. 31, figs 8, 10). This groove continues up to the peristome and is widest near the top of the anterior sulcus becoming narrower towards the base of the sulcus. Pore-pairs are oblique isopores, closely spaced in the upper half, but becoming smaller and more widely spaced towards the bottom of the sulcus. The margins of the sulcus are relatively sharp, especially towards the top of the anterior sulcus, where they may form small crests on either side. The width of the sulcus is 13–20% of the test width (mean = 16·3%, SD = 1·86%, N = 12) and at its deepest it is about 3·5 to 4·5 mm.

The anterior petals are strongly asymmetric, with only the posterior column well-developed (Pl. 31, fig. 8; Fig. 77). These curve forward and, towards the tip, turn slightly down. The inner pore is circular, the outer one elongate, and the distance between the pairs is as wide as the outer slit-like pore. Pore-pairs are conjugate and are separated from one another by a single row of small tubercles. The posterior column tapers both adapically and adambitally. There are 45 pore-pairs in a column in a 65 mm individual, rising to 52 in an 81 mm individual (Fig. 76). The anterior column of pores remains rudimentary throughout. All are pore-pairs, but the pores always remain small and close together, never becoming conjugate. However, they do gradually increase in size towards the ambitus.

The posterior petals are similar to the anterior petals in their pore-pair development and column asymmetry, with only the posterior column bearing large conjugate pore-pairs (Fig. 77). This column is flexed outwards and backwards and extends only about two thirds of the distance towards the ambitus. There are 32 pore-pairs in a column in a 65 mm individual, rising to 42 in an 81 mm individual. Close to the apex the two ambulacra are almost parallel, but further away they diverge at about 90°. Pores beneath the petals remain double, but are microscopic. Close to the mouth there are

two to three larger peribuccal pores in ambulacrum III, four to five in ambulacra II and IV, and three to four in ambulacra I and V.

The interambulacra are biserial to the apex, although they become extremely narrow, especially posteriorly. On the oral surface there is a short, broad labral plate followed by a series of 5 alternating triangular-shaped plates which either just or almost reach the opposite suture (Fig. 77). Further towards the posterior the columns become more typically biserial.

The peristome is oval, slightly more than twice as wide as long, and lies at the base of the anterior sulcus, some 15–18% of test length from the anterior (mean = 17%, SD = 1·2%, N = 11). The peristome faces forward and is visible in anterior view. The labral plate hardly indents the posterior of the peristome.

The periproct is oval, typically about 70% as wide as tall, and is strongly overhung so that it is visible from the oral surface but not from the apical surface (Pl. 31, figs 8, 9). The test beneath the periproct is indented and there are two projections on either side. The periproct opens between interambulacral plates 5 and 10, the lower plates being strongly curved. The periproct lies low on the posterior surface and the distance to the base of the periproct from the lower surface is some 18–27% of the test height.

Tuberculation is fine and uniform throughout, except along the inner (interambulacral) margin of the frontal sulcus where a double or triple row of noticeably larger tubercles is developed. There is no trace of a lateral fasciole to be seen. Oral tubercles are slightly larger than adapical ones, but there is no real difference in size between the tubercles of the plastron and those of the latero-ventral regions. The oral ambulacra appear to be tubercle-free.

Remarks. This species is relatively common at certain levels in Jebel Rawdah. It co-occurs with small varieties of *H. persicus* but can be distinguished from that species by its narrower, more vertical and more sharply defined anterior sulcus, its more anterior apical disc, its lack of adapical primary tubercles, and its more quadrate profile. It differs from *H. arabicus*, whose size range is more-or-less coincident, in having the apical disc positioned anterior of centre, and in having a more developed vertical component to the anterior sulcus.

The stratigraphically lowest species tend to have a more rounded profile, while higher samples become progressively more peaked, with a stronger posterior inclination as the region immediately in front of the apical disc becomes taller. Thus in the beds immediately above bed 13, Jebel Rawdah, section 2, *H. compressus* is rather flat and the vertical component of the anterior sulcus is small. By bed 21 the tests are much more quadrate in outline, with a small but obvious peak in front of the apical disc, and by bed 26 some highly elevated tests are found.

Hemipneustes persicus Cotteau & Gauthier, 1895 Pl. 31, figs 1–7; Pl. 32, figs 1–4; Figs 76, 78D, 79

1895 *Hemipneustes persicus* Cotteau & Gauthier: 15, pl. 2, figs 1–6.
1895 *Hemipneustes minor* Cotteau & Gauthier: 17, pl. 2, figs 7–9.
1921 *Hemipneustes sardanyolae* Vidal: 11, pl. 2, fig. 2; pl. 3, fig. 2.

Types. The syntypes are the specimens from Aftab and Derre-i-Chahr, Iran, described by Cotteau & Gauthier (1895: 15). Although the authors stated that they had many examples, their description appears to have been based on only one specimen 54 mm in length, which was illustrated. This is here designated lectotype.

Material studied. There are five large individuals of this species, BMNH EE4083, EE4084, EE4090, EE5025–26, all rather poorly preserved. Small individuals that appear indistinguishable are relatively common and well-preserved at one horizon at Jebel Rawdah, section 2. Biometric data is based on the following eleven specimens: BMNH EE3742, EE3746–47, EE4091, EE4097, EE4099, EE5028–32 in addition to the five larger specimens cited above.

Occurrence. In the Oman Mountains region this species

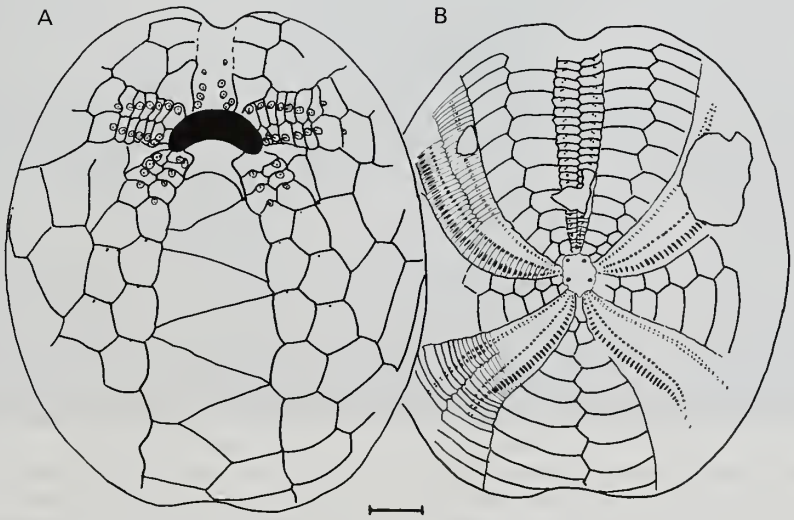


Fig. 79 Camera lucida drawing of plating in *Hemipneustes persicus* Cotteau & Gauthier. **A**, oral surface, BMNH EE3747; **B**, apical surface, BMNH EE3746. Scale bar = 5 mm.

occurs at Jebel Rawdah at the following localities and horizons:
Section 1: bed 4 (2).
Section 2: bed 19 (1); beds 20/21 (23); loose in scree, derived from beds 14–21 (4).
Section 3: bed 5 (1); bed 7 (1).
Section 4: loose a little below the top of the measured section (1).

The type series comes from the 'Senonienne' (probably Maastrichtian) of Aftab and Derre-i-Chahr, southern Iran.

DIAGNOSIS. Test ovate, depressed in side-view and in cross-section arched. Width 80–88% of length, mean = 85%: height 42–55% of length, mean = 49% [size range 44–89 mm test length]. Frontal groove broad and open, expanding anteriorly, comparatively shallow at the anterior; never keeled. Apical disc lies approximately mid-length (distance between anterior and apical disc 45–52% of test length; mean = 48%). Distinguished from other species by (i) its depressed, rounded profile, (ii) broad, relatively shallow anterior groove (iii) central apical disc.

DESCRIPTION. Tests range from 44 to 89 mm in length and from 38 to 68 mm in width (width = 80–88% of length; mean = 85%, SD = 2·1%, N = 4). In outline the test is oval with a prominent anterior sulcus and a truncated posterior (Pl. 31, figs 1, 3, 4, 6). The widest point on the test is approximately mid-length. In profile the test is depressed, more or less uniformly curved both in front and behind, with the tallest point of the test anterior of centre (Pl. 31, figs 2, 5). Test height is 42–53% of length (mean = 48%, SD = 4·2%, N = 5). In anterior profile the sides are uniformly rounded.

The apical disc lies approximately mid-length, 43–52% of test length from the anterior border (mean = 48%, SD = 2·4%, N = 15). Plating appears to be similar in arrangement to that of *H. compressus*, with the anterior pair of genital plates separated from the posterior pair by ocular plates II and IV, which meet centrally (Fig. 78D). Madrepores extend over genital plates 2 and 3, and over ocular plates II, III and IV.

The pores of the anterior groove are small and closely spaced adapically, becoming slightly more widely separated towards the ambitus. The anterior sulcus is rather broad and shallow, becoming more or less parallel-sided towards the anterior border (Pl. 31, figs 1, 3, 6). The margins of the groove are gently rounded, never crested. The width of the sulcus is 17–22% of the test width (mean = 19%, SD = 2·0%, N = 13) and at its deepest it is only 2·0–3·0 mm in depth. The sulcus does not have a vertical component at the anterior, as is seen in *H. compressus*, but curves uniformly towards the ambitus.

Petals are as in *H. compressus*, though the anterior pair are slightly more curved forwards than in that species (Fig. 79). The anterior column of pore-pairs in each petal is composed of small, rudimentary pore-pairs which become slightly larger towards the ambitus. The posterior column in each petal is composed of wide, conjugate pore-pairs, with the inner pore circular and the outer pore distinctly slit-like. There are 36 pore-pairs in the posterior column of ambulacrum II petal, and 28 in ambulacrum I petal in a 44 mm length individual, rising to 65 and ?55 pore-pairs respectively in an 80 mm individual. The anterior petals curve forwards to diverge at an angle of approximately 30° to the midline, before tapering and turning laterally slightly at their distal end. They extend almost to the ambitus in adapical view (Fig. 79). The posterior petals are slightly shorter, extending approximately two-thirds of the distance to the ambitus. They too are flexed, but for most of their length they diverge at approximately 50° to the midline. Pores below the petals are microscopic, but remain double. Peribuccal pores are well-developed, with four or five to a column in ambulacrum III, six or seven in ambulacra II and IV, and four or five in ambulacra I and V.

The interambulacra become very narrow adapically (Fig. 79), but remain biserial. The plastron consists of a small, broad, labral plate followed by five wedge-shaped plates arranged uniserially (Fig. 79).

The peristome is oval to crescentic, slightly more than twice as wide as long, and lies at the base of the anterior sulcus, some 17–21% of test length from the anterior (mean = 19%, SD = 1·8%, N = 5). The labral lip projects downwards slightly and is visible in anterior view. The labral plate indents the posterior of the peristome.

The periproct is oval, 65–75% as wide as tall (mean = 71%), and more or less vertical on the posterior face. It is therefore not visible from either the apical or oral surfaces (Pl. 31, figs 1–4). There are no subanal protuberances developed in small individuals, although small protruberances are found on larger individuals (Pl. 32, fig. 2). The periproct opens between interambulacral plates 5 and 10, the lower plates being strongly curved. The periproct lies low on the posterior surface and the distance to the base of the periproct from the lower surface is some 16–25% of the test height (mean = 22%).

Aboral tuberculation consists of small primary tubercles scattered amongst dense miliaries. Larger primary tubercles are found along the inner (interambulacral) margins of the frontal sulcus, where they are approximately three abreast. They are also found close to the apical disc interambulacrally on many juveniles. These adapical tubercles are only slightly larger than other tubercles, but form a characteristic feature where preservation is good. There is no trace of a lateral fasciole. Oral tubercles are slightly larger than adapical ones, but there is no real difference in size between the tubercles of the plastron and those of the latero-ventral regions. The plastron tubercles are largest towards the adambulacral margins and decrease in size towards the midline. Oral ambulacra are smooth and free of tubercles.

REMARKS. I have examined topotype material of this species from Iran and feel secure that the Omani Mountain material is conspecific. However, there is one small difference; the Omani specimens in general have a slightly shallower anterior groove at the ambitus than do the Iranian specimens. This is not considered sufficient to merit separation, since all intermediates can be found. Similarly, *Hemipneustes sardanyolae* Vidal from the late Campanian of Sardanol, Spain, is slightly flatter and more oval in outline, but is otherwise very similar. It too is synonymized here.

The species is readily distinguished from *H. compressus* by its very different, more depressed profile, shallower and very much broader frontal sulcus and central apical disc. It also has better developed phyllodes. It differs from *H. arabicus* in its very broad and shallow frontal sulcus, and from *Opisopneustes* in the lack of aboral primary tubercles.

There is little doubt that the closest species to *H. persicus* is *H. delettrei* (Peron & Gauthier) from the late Campanian of North Africa. Both have a very similar broad, shallow frontal

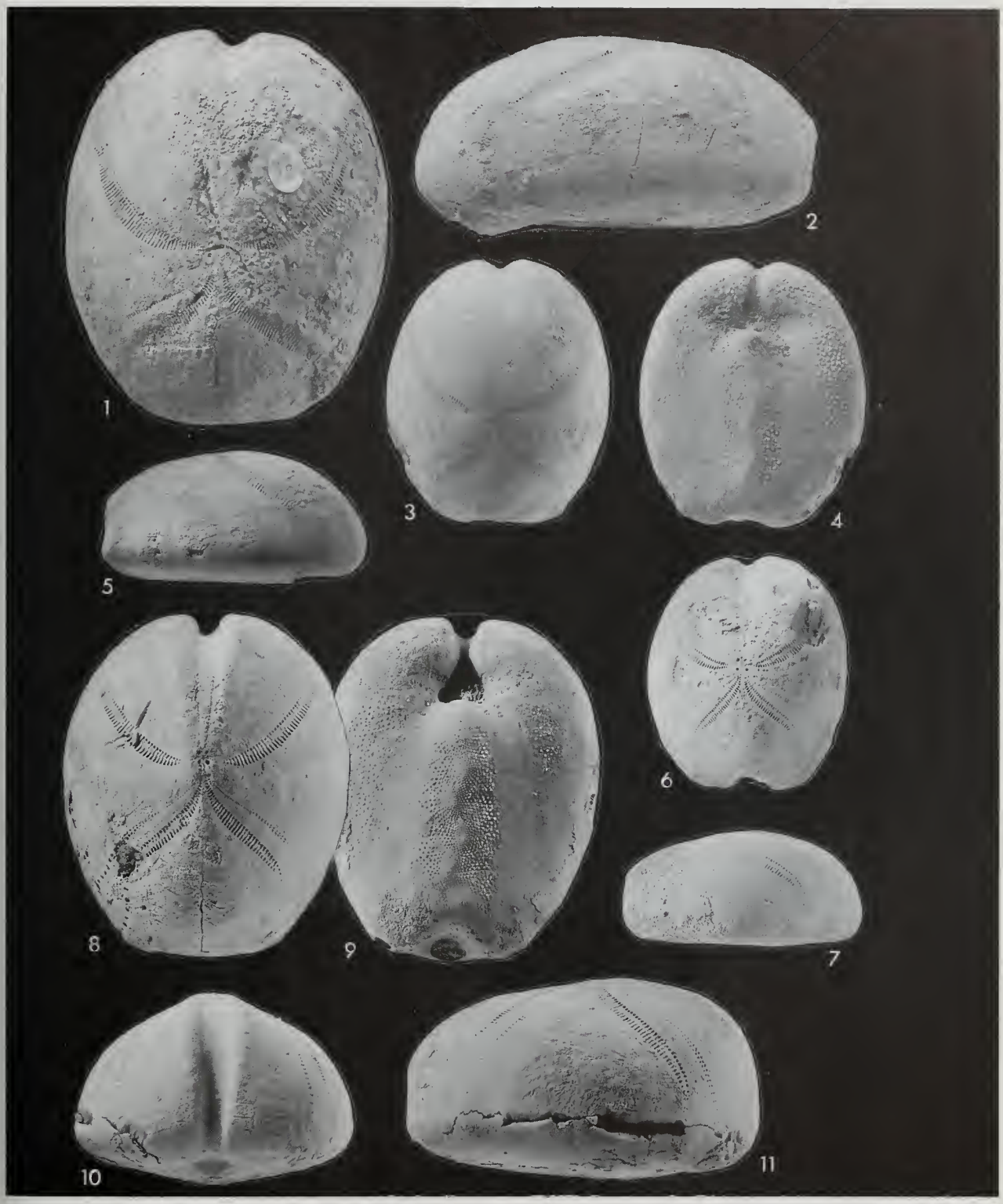


PLATE 31

Figs 1–7 *Hemipneustes persicus* Cotteau & Gauthier. **1, 2,** BMNH EE4084; **1**, apical; **2**, lateral; both × 1. Jebel Rawdah, section 3, bed 5. **3–5,** BMNH EE5032; **3**, apical; **4**, oral; **5**, lateral; all × 1. Jebel Rawdah, section 2, bed 21. **6,** BMNH EE3746, apical, × 1. Jebel Rawdah, section 2, bed 21. **7,** BMNH EE3747, lateral, × 1. Jebel Rawdah, section 2, bed 21.

Figs 8–11 *Hemipneustes compressus* Noetling. BMNH EE3745; **8**, apical; **9**, oral; **10**, anterior; **11**, lateral; all × 1. Jebel Rawdah, section 2, bed 21.

groove that expands continuously towards the anterior, a character seen in no other *Hemipneustes*. *H. persicus* differs from *H. deletrettei* primarily in being very much more depressed in profile and more elongate, with more strongly inflexed petals. However, the differences are not great.

Hemipneustes arabicus Ali, 1989 Pl. 30, figs 1–4; Figs 76, 78B, 80

1989 *Hemipneustes arabicus* Ali: 408, figs 6 (1–3), 7.
1989 *Hemipneustes persicus* Cotteau & Gauthier; Ali: 408, fig. 6 (4).

TYPES. The syntype series are the seven specimens and three fragments mentioned by Ali (1989) as being housed in the Geology Department Museum, Al Ain University, United Arab Emirates. The lectotype, here designated, is his figured specimen (*op. cit.* fig. 6 (1–3)).

MATERIAL STUDIED. Nine specimens: the following description is based on the four best-preserved of these, BMNH EE4085, EE4087–88, EE5027.

OCCURRENCE. This species was first described from Jebel Rawdah, Oman. Specimens were collected from the following horizons at Jebel Rawdah:
Section 1: bed 4 (3).
Section 2: bed 11 (4); bed 14 (1).
Section 4: loose in scree, a little below beds 21/22 (1).

DIAGNOSIS. Test ovate and rather elongate, depressed in side-view and in cross-section arched. Width 76–79% of length, mean = 77%; height 45–46% of length, mean = 45% (size range 76–89 mm). Frontal groove narrow, sharply defined with a small but prominent rim; deeply sunken at the anterior. Apical disc lies at or slightly behind mid-length (distance between anterior and apical disc = 49–55% of test length: mean = 52%). Distinguished from other species by (i) its depressed, elongate profile, (ii) long, sharp and deep anterior groove (iii) central apical disc.

DESCRIPTION. Tests range in length from 77 to 89 mm and in width from 60 to 69 mm (width = 76–79% of length, mean = 77%, SD = 1·1%, N = 4). The widest point lies at or slightly in front of mid-length. In outline the test is oval with a sharp and narrow anterior sulcus and a rather broad posterior truncation (Pl. 30, fig. 1). In side-view the test is depressed and gently rounded (Pl. 30, fig. 4). Test height is 44–46% of length (mean = 45%, SD = 0·8%, N = 4). The tallest point on the test is at, or slightly in front of, the apex. In anterior view the test is uniformly rounded, but there are small crests on either side of the sulcus.

The apical disc is clearly seen in BMNH EE5027 (Fig. 78B). Genital pores are large and separated, with ocular plates II and IV meeting centrally and separating genital plates 2 and 3 from genital plates 1 and 4. Madrepores cover genital plates 2 and 3 and ocular plates II, III and IV. A couple of pores also appear on the margin of genital plate 1. It lies 49–55% of the test length from the anterior border (mean = 52%, SD = 2·5%, N = 4).

Ambulacrum III is narrow and parallel-sided adapically (Pl. 30, fig. 2). It is slightly depressed from the apex until it approaches the anterior border, then it turns rather sharply downwards into a deep groove, 4–6 mm in depth. The sulcus remains narrow throughout, only 11–16% of the test width at the anterior (mean = 13%). Pore-pairs are densely packed along its length until it turns adorally, where they become much more spread out. The floor of the sulcus is covered in fine tuberculation which decreases in size away from the pore-pairs towards the perradius.

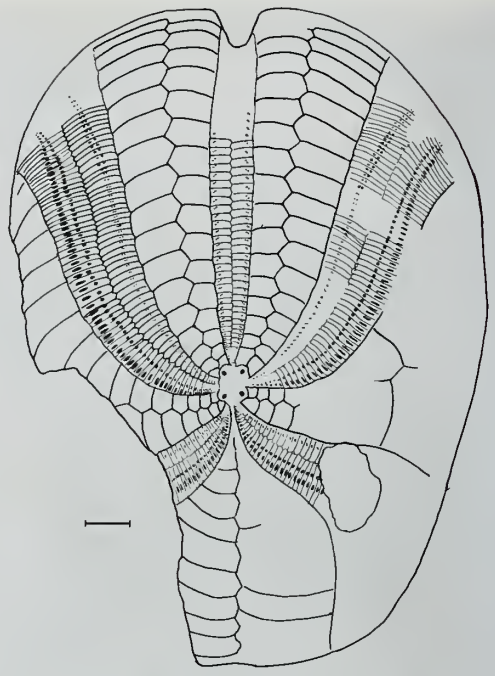


Fig. 80 Camera lucida drawing of adapical plating of *Hemipneustes arabicus*, BMNH EE5027. Scale bar = 5 mm.

The petals are similar in form to those of other species of *Hemipneustes*, the adapical pores in the anterior columns being particularly rudimentary. The anterior petals are flexed forward and diverge at an angle of about 15° to the frontal groove before curving laterally near their distal end (Fig. 80). The posterior petals diverge at about 110–120° to each other. Adorally there are well-developed phyllodes, with five or six pores in a column in the lateral ambulacra.

The plastron consists of a small, broad labral plate and a series of four or five wedge-shaped plates that extend across the full width of the plastron (Fig. 80). Posterior plates are biserial. The peristome is oval, indented slightly by the labral plate, and predominantly forward-facing. It lies at the base of the anterior sulcus, some 16% of the test length from the anterior border.

The periproct is oval and downward facing; clearly visible from below but hidden from above (Pl. 30, figs 1, 2). The test is developed into two prominent bulges, one on either side of the periproct. The periproct lies between interambulacral plates 5 and 10. The base of the periproct lies between 19 and 26% of the test height above the base.

Tuberculation is fine and uniform over the apical surface, except along the inner interambulacral margins of the frontal groove, where larger primary tubercles are developed. Oral tuberculation is slightly coarser, with ambulacral zones free of any tuberculation. No lateral fasciole is seen.

REMARKS. This species appears somewhat intermediate between the broad grooved *H. persicus* and the tall, narrow-grooved but upright *H. compressus*. It differs from *H. persicus* in the sharpness and narrowness of its anterior

PLATE 32

Figs 1–4 *Hemipneustes persicus* Cotteau & Gauthier. Specimen in the Morgan Collection, Museum d'Histoire Naturelle, Paris; **1**, apical; **2**, oral; **3**, lateral; **4**, anterior; all × 2. Arkouraj, Iran.

Figs 5–8 *Hemiaster hattaensis* Ali. **5**, BMNH EE4060; apical, × 2. Jebel Thanais, basal 2 m of the Simsima Formation. **6–8**, BMNH EE4059; **6**, lateral; **7**, apical; **8**, oral; all × 1·5. Jebel Buhays, section 1; loose in the scree derived from the lowest 3 m of the Simsima Formation.

sulcus. In *H. persicus* the frontal groove is much broader and lacks the interambulacral keels. It is also much less deeply indented at the ambitus. However, like *H. persicus*, *H. arabicus* has its apical disc at or slightly behind mid-length, in contrast to *H. pyrenaicus* where the test is more quadrate and the apical disc lies anterior of centre. Like *H. compressus*, *H. arabicus* shows a sharp change from apical to anterior sectors of its anterior sulcus.

Order **SPATANGOIDA** Claus, 1876
Family **HEMIASTERIDAE** Clark, 1917
Genus ***HEMIASTER*** Agassiz, in Agassiz & Desor, 1847

Hemiaster hattaensis Ali, 1989 Pl. 32, figs 5–8; Figs 81C–E

?1903 *Hemiaster* sp. Lambert: 87, pl. 3, figs 6–8.
1989 *Hemiaster (Bolbaster) hattaensis* Ali: 409, fig. 6 (5–8).

TYPES. Eleven specimens referred to by Ali form the syntype series since no holotype was designated. These are in the Geology Department Museum, University of Al Ain, United Arab Emirates.

MATERIAL STUDIED. Thirteen specimens, of which the following six were used for the biometric study: BMNH EE4055, EE4057, EE4059–60, EE4064 and EE4320.

OCCURRENCE. The species is known for certain only from the western Oman mountain. It has been found at the following localities:
Jebel Buhays, section 1: loose in the scree, derived from the lowest few metres of the Simsima Formation (5).
Jebel Thanais: lowest 2 metres of the Simsima Formation (1).
Jebel Rawdah, section 1: bed 6 (3).
Jebel Rawdah, section 2: loose in scree (1).
Jebel Rawdah, section 3: bed 5 (1).
Jebel Rawdah, section 4: bed 2 (1); bed 13 (1).

DIAGNOSIS. An ovate *Hemiaster* with cruciform petals in which the posterior pair are about half the length of the anterior pair. Apical disc ethmophract, with the posterior genital plates L-shaped and separating the posterior ocular plates; lying posterior to midlength. Ambulacrum III long, narrow, depressed adapically but becoming flush with surrounding area towards the ambitus.

DESCRIPTION. Tests oviform with a uniformly rounded anterior and a slightly pointed posterior (Pl. 32, fig. 5). Test length is 15–32 mm and test width 11–26 mm (width = 82–87% of length in larger individuals but only 75% in a juvenile 15 mm long). The widest point lies about mid-length. Test rather depressed in profile (Pl. 32, fig. 6), with a height 55–67% of length (mean = 64%, SD = 4·6%, N = 6). Lower surface gently convex with a slight keel to the plastron towards the peristome. Upper surface flat towards the posterior, sloping uniformly towards the anterior (Pl. 32, fig. 6). The tallest point on the test lies just posterior to the apical disc.

The apical disc is ethmophract (Fig. 81D) and lies 58–62% of the test length from the anterior border in adults, but further (73%) in the juvenile 15 mm in length. Anterior gonopores are set closer together than the posterior pair. Genital plates 2 and 3 are relatively small whereas genital plates 1 and 4 are longer and L-shaped and are broadly in contact (Fig. 81D). There are relatively few madrepores developed. Ocular plates are small, pentagonal and project.

The anterior ambulacrum is sunken adapically but the sulcus is lost about two-thirds of the way towards the ambitus and there is no indentation at the ambitus (Pl. 32, figs 5, 7). The adapical sulcus is parallel-sided and very narrow. There are 14 pore-pairs in a column in 17–18 mm individuals and these are strongly oblique with a prominent interporal partition. The floor of the sulcus is covered in fine and dense granulation. Pores beyond the peripetalous fasciole are single and minute. The interambulacra on either side of the frontal sulcus are keeled, especially in the larger specimens.

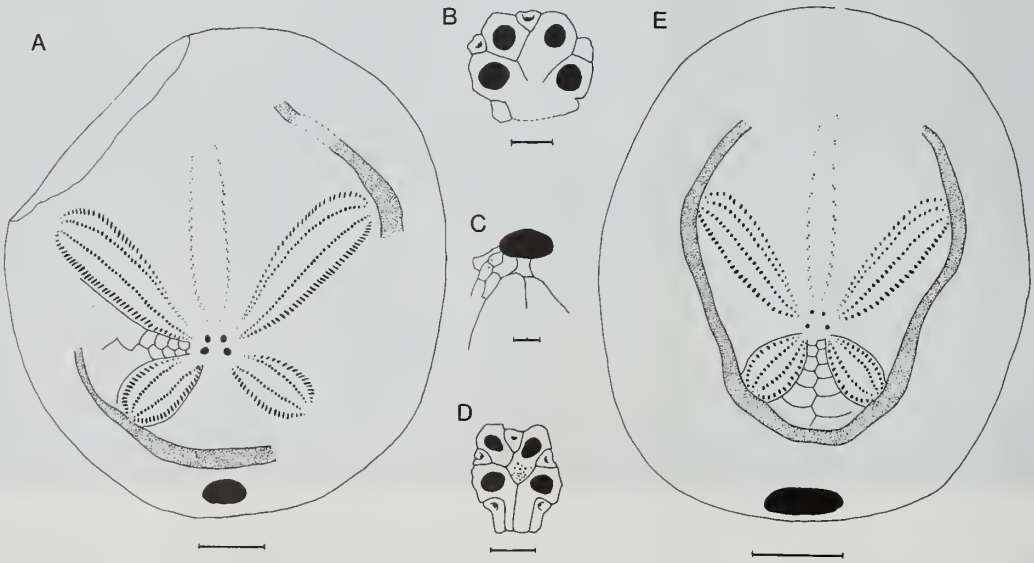


Fig. 81 Camera lucida drawings of plating in *Hemiaster* species. **A, B**, *Hemiaster paronai* Checchia-Rispoli, BMNH EE5034: A, apical surface (fasciole stippled); B, apical disc. **C-E**, *Hemiaster hattaensis* Ali: C, peristome and labral plate, BMNH EE4064; D, apical disc, BMNH EE4060; E, apical surface (fasciole stippled), BMNH EE4059. Scale bars: A, E = 5 mm; B, D = 1 mm; C = 2 mm.

The petals are cruciform and sunken, the anterior pair being twice as long as the posterior pair (Pl. 32, figs 5, 7; Fig. 81E). Pore-pairs are broad and conjugate and the columns close distally. The perradial zone is slightly narrower than the pore-pair zones on either side. There are 12–14 pore-pairs in a column in the posterior petals and 24–26 in the anterior petals in individuals 15–18 mm in length.

The periproct is tear-drop shaped, pointed adapically, and lies high on the posterior face. It is about 3 mm wide and 4 mm in height in an individual 17 mm in length. The base of the periproct lies 55–58% of test height above the base.

The peristome is D-shaped and is 1·6 to 1·8 times as broad as wide. It lies 24–29% of the test length from the anterior border in 17–18 mm length individuals. It is neither invaginated nor does it have a surrounding rim, as is seen in many *Hemiaster* species. The plastron is broad, with a straight, median suture (Fig. 81C). It is covered in dense orderly rows of tubercles. The labral plate is vase-shaped and relatively small. Surrounding the peristome there are four phyllode pores in each column of a lateral ambulacrum and three in the posterior ambulacrum. There are also two or three enlarged subanal pore-pairs.

There is a well-developed peripetalous fasciole that is without sharp angles. The remainder of the upper surface has scattered primary tubercles and dense miliaries.

REMARKS. Ali (1989) erected this species for 11 specimens from Jebel Rawdah. It resembles *H. aquisigranensis* Schlüter in the form of its petals and frontal groove, but differs from that species in having a larger peristome and having a vertical or slightly outward-sloping posterior. In *H. aquisigranensis* the posterior is strongly retrenched, such that the periproct is visible from the oral surface rather than the aboral surface. *H. hattopsis* undoubtedly comes closest to *H. punctatus* d'Orbigny, from the late Campanian of France. However, this species differs in being very much smaller, more elevated and in having a well developed rim to the peristome.

Lambert (1903) described and figured a badly preserved specimen that may be conspecific. Lambert's specimen came from the late Cretaceous of Fanivelona, eastern Madagascar. It has a very similar overall shape, but unfortunately the apex of the test is damaged and only the anterior petal on one side is preserved. It is only tentatively assigned to this species.

Hemiaster paronai Checchia-Rispoli, 1921 Pl. 33, figs 1–4; Figs 81A, B

1921 *Hemiaster Paronai* Checchia-Rispoli: 27, pl. 8, fig. 24, pl. 9, figs 14–18.
1932 *Hemiaster Paronai* Checchia-Rispoli; Checchia-Rispoli: 8, pl. 2, figs 1–8.
?1967 *Hemiaster punctatus* d'Orbigny; Devries: 194, pl. 6, figs 34–41.
?1967 *Hemiaster regulusanus* d'Orbigny; Devries: 194, pl. 6, figs 42–44.

MATERIAL. Seven specimens, only one of which is well-preserved, BMNH EE5034.

OCCURRENCE. Specimens were found at the following localities and horizons in the western Oman mountains:
Jebel Huwayyah, section 1: bed 9 (1); bed 11 (1).
Jebel Huwayyah, section 2: beds 3–5 (3).
Jebel Faiyah, section 1: bed 4 (1).
Jebel Rawdah, section 3: bed 9 (1).
Elsewhere the species has been recorded from the Maastrichtian of northern Libya.

DIAGNOSIS. Like *H. hattaensis* but more inflated and more circular in outline, with deeper petals and deeper and wider anterior sulcus adapically.

DESCRIPTION. The best preserved specimen is 37·1 mm in length, 35·6 mm in width (96% of length: widest point approximately mid-length) and 28·8 mm in height (78% of length). In outline the test is more or less circular and in profile the upper and lower surfaces are broad and flat with the anterior uniformly rounded and the posterior sloping steeply outwards (Pl. 33, figs 1–4).

The apical disc is ethmophract with the posterior two genital plates rather stout and broadly in contact (Fig. 81B). The posterior ocular plates are separated. Gonopores are large and occupy most of the plate, but in some individuals (?males) may be relatively smaller. Genital plate 2 has a small central zone of madrepores. The apical disc lies 58% of the test length from the anterior border.

The anterior ambulacrum lies in a frontal sulcus which is bordered by sharp interambulacral crests adapically but which shallows and is lost towards the ambitus (Pl. 33, fig. 2). There are 22 pore-pairs in a column between the apex and the peripetalous fasciole and these are strongly oblique. The sulcus is rather narrow and slightly lanceolate in outline.

The petals are cruciform with the anterior pair twice the length of the posterior pair (Fig. 81A). There are 40 pore-pairs in a column in the anterior pair and 21 in the posterior pair at 37 mm test length. Petals close distally and the perradial interporal zone is narrower than either of the bordering pore zones.

The periproct is oval, slightly pointed adapically and lies high on the posterior side. It is just visible from above because of the outward slope of the posterior face. It is about 70% as wide as tall and is 18% of the test height in height. Its base lies 60% of test height above the base (Pl. 33, fig. 4).

The peristome is D-shaped, twice as wide as long and lies 28% of the test length from the anterior border. It is not rimmed. There are five phyllode pores in each column of lateral and posterior ambulacra. There are also five subanal pore-pairs in the two posterior interambulacra.

REMARKS. This species closely resembles *H. hattaensis* in the shape of petals, apical disc structure and the form of the anterior ambulacrum. However, it differs consistently in shape, being both more rounded in outline and more inflated in profile. This is not simply an attribute of size, since the small specimens from Jebel Huwayyah (eg. BMNH EE4061, 22 mm in length) are very different in shape from similar-sized individuals from Jebel Buhays. In addition the pore-pairs in the frontal groove are more numerous and more densely packed.

The specimens appear indistinguishable from those described from the Maastrichtian of Libya by Checchia-Rispoli (1921) under the name *H. paronai*. Very similar material was also described by Devries (1967) from the Maastrichtian of Turkey under the names *Hemiaster punctatus* d'Orbigny and *H. regulusanus* d'Orbigny. Unlike the specimens described here and by Devries (1967), *H. punctatus* has a large flush peristome lacking a rim. The species is also very similar to *Hemiaster noemiae* Cotteau & Gauthier, from the late Senonian of southern Iran (Pl. 33, figs 5–8). However, *H. noemiae* differs in having a shorter anterior

PLATE 33

Figs 1–4 *Hemiaster paronai* Checchia-Rispoli. BMNH EE5034; **1**, oral; **2**, apical; **3**, lateral; **4**, posterior; all × 2. Jebel Rawdah, section 3, bed 9.

Figs 5–8 *Hemiaster noemiae* Cotteau & Gauthier. B18727, Morgan Collection, Museum d'Histoire Naturelle, Paris; **5**, oral;**6**, apical; **7**, posterior; **8**, lateral; all × 2. Senonian of Awasa, Iran.

Figs 9–11 ?*Linthia sudanensis* (Bather). BMNH EE4054; **9**, lateral; **10**, apical; **11**, oral; all × 1·5. Loose near top of section at Jebel Rawdah, section 3.

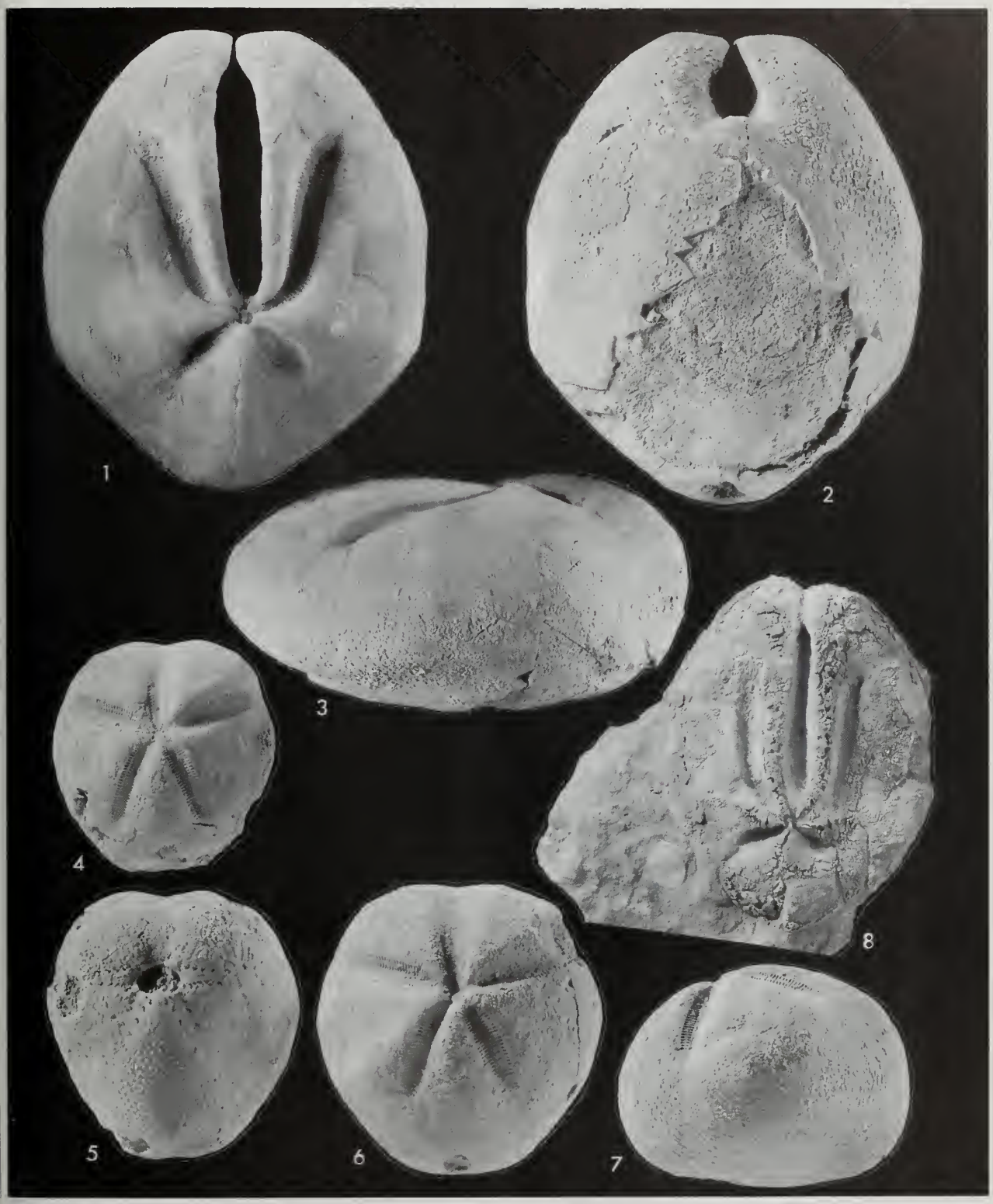


PLATE 34

Figs 1–3, 8 *Proraster geayi* Cottreau. **1–3,** specimen in Museum d'Histoire Naturelle, Paris; **1**, apical; **2**, oral; **3**, lateral; all × 2. Maastrichtian of Antanihody, Madagascar. **8,** BMNH EE4067, apical, × 1. Jebel Huwayyah, section 1, bed 18.

Figs 4–7 *Mecaster victoris* (Lambert). Jebel'Rawdah, section 3, bed 5. **4,** BMNH EE4050; apical, × 2. **5,** BMNH EE4049; oral, × 2. **6, 7,** BMNH EE4042; **6**, apical; **7**, lateral; both × 2.

sulcus with many fewer pore-pairs, and in having a much smaller peristome at comparable sizes.

Genus *MECASTER* Pomel, 1883

Mecaster victoris (Lambert, 1932) Pl. 34, figs 4–7; Figs 82–84A

1932 *Hemiaster Victoris* Lambert: 127, pl. 4, figs 18, 19.
1967 *Hemiaster* sp. Devries: 194, pl. 6, figs 45–47.
1990 *Periaster subsexangulatus* Airaghi; Ali: 410, fig. 5 (8).

MATERIAL STUDIED. Ten reasonably complete specimens were used in the biometric analysis, BMNH EE4035–36, EE4038–40, EE4042, EE4045–46, EE5035–36. Another 32 specimens were collected.

OCCURRENCE. In the study area, this species was found at the following localities and horizons:
Jebel Buhays, section 1: loose in the scree, derived from the lowest few metres of the Simsima Formation (1).
Jebel Huwayyah, section 1: bed 14 (1).
Jebel Huwayyah, section 2: beds 3–5 (3).
Jebel Rawdah, section 3 (top of bed 5 (28): bed 8 (2); beds 9/10 (7).

The species was originally described from the Campanian of El Kantara, Algeria. A poorly preserved specimen that also appears identical was described from the Maastrichtian of Cortinek, Turkey.

DESCRIPTION. Specimens range in size from 24 to 33 mm in length. Mean test width is 98% of the length (range 93–100%, SD = 3·2%, N = 9) and test height 76% of the length (range 72–80%, SD = 3·1%, N = 7). The test is weakly cordiform in outline, tapering posteriorly to a rounded point and with the widest point in front of the mid-line (Pl. 34, figs 4–6). In profile the test is inflated with a rounded posterior and anterior (Pl. 34, fig. 7). The tallest point is posterior of the apical disc.

The apical disc lies 36–40% of the test length from the anterior border (mean = 38%, SD = 1·4%, N = 8). It is ethmolytic with the posterior oculars separated by the madreporite (Fig. 84A). The gonopores on each side of the mid-line lie close together.

Although ambulacra are sunken, they are all rather shallow and relatively narrow (Pl. 34, figs 4, 6; Fig. 83A). Pore-pairs in the anteal sulcus are small and situated along the adradial margins. The anterior petals are long, narrow and straight-sided. They extend most of the way to the ambitus and diverge from one another at an angle of 130°. There are 33 pore-pairs in a column at 25 mm test length, rising to 36 at 29 mm test length. The pore-pairs are narrow, with the outer pore in each pair slightly more elongate than the inner. The posterior petals extend about 75% of the distance to the ambitus and are equally narrow and parallel-sided. They are about 85-90% of the length of the anterior petals and have 28 pore-pairs in a column at a test diameter of 25 mm, rising to about 32 at 28 mm.

The periproct is high on the posterior and is usually just visible from above. The base lies more or less half way up the posterior face (mean = 50%, SD = 4·5%, N = 4). The opening is vertically elongate, being about 1·6–1·8 times as tall as broad, and is pointed adapically.

The peristome is D-shaped and lies about 20% of the test length back from the anterior border (range 18·5–21·5%, SD = 1·1%, N = 6). The labrum projects slightly over the opening. The labral plate is relatively long and narrow, almost parallel-sided (Fig. 83B). It meets only one of the sternal plates.

Tuberculation is fine adapically, slightly coarser adorally. There is always a peripetalous fasciole, some 0·6 mm in width. Although preservation is usually too poor to allow its course to be traced fully, there appears to be little indentation of the peripetalous fasciole laterally and it runs close to the ambitus. In one specimen (BMNH EE4050) there is a distinct latero-anal fasciole also, but other specimens, equally well preserved in this region have only rudimentary traces of such a fasciole or no fasciole at all. It is clear that the latero-anal fasciole is variably developed in this species.

REMARKS. Lambert (1932: 127) created this species on the basis of material from the late Campanian of El Kantara, Tunisia. It has narrower, shallower petals than other *Mecaster* species and in profile is inflated with the tallest point lying well to the posterior. Lambert noted that there were traces of a latero-anal fasciole in six out of twelve specimens, while another three had a distinct latero-anal fasciole. Lambert separated those with a latero-anal fasciole and placed them in his '*Periaster Victoris*', though recognising that they were completely intergradational with *Hemiaster victoris*. As Lambert quite correctly pointed out, the presence/absence of a latero-anal fasciole is highly variable and the various species classified under the genus *Periaster* are polyphyletic in origin.

Ali (1989) figured a specimen of this species without description under the name *Periaster subsexangulatus* Airaghi. However, *P. subsexangulatus* has a much broader, deeper anteal sulcus, is less rounded and less inflated and most particularly, the petals are broader and less parallel-sided and the posterior pair are distinctly shorter than the anterior pair.

The plastron structure is significant in that the labral plate is in contact with sternal plate 2b only (Fig. 83B). This is also the situation in *Iraniaster* and other Somaliasteridae. *Iraniaster* has been placed in the Holasteroida on account of its plastron structure, yet it has a compact apical disc in which the posterior genital plates, but not the posterior ocular plates, are separated by the madreporite (Kier 1972, figs 41–42). The fact that a meridoplacous plastron can be developed in at least one *Mecaster* species, and the similarity of apical disc plating strongly indicates that somaliasterids are derived from the *Mecaster* lineage.

Family **SCHIZASTERIDAE** Lambert, 1905
Genus **LINTHIA** Desor, 1853

?Linthia sudanensis (Bather, 1904) Pl. 33, figs 9–11; Figs 84B, 85

?1904 *Hemiaster sudanensis* Bather: 299, pl. 11, figs 6–13.

MATERIAL. One specimen, BMNH EE4054.

OCCURRENCE. The specimen was found loose about 8 m below the top of section 3 at Jebel Rawdah, western Oman. The section here is capped by a two metre thick conglomerate of reworked Simsima Limestone and thus the specimen could be of late Maastrichtian age.

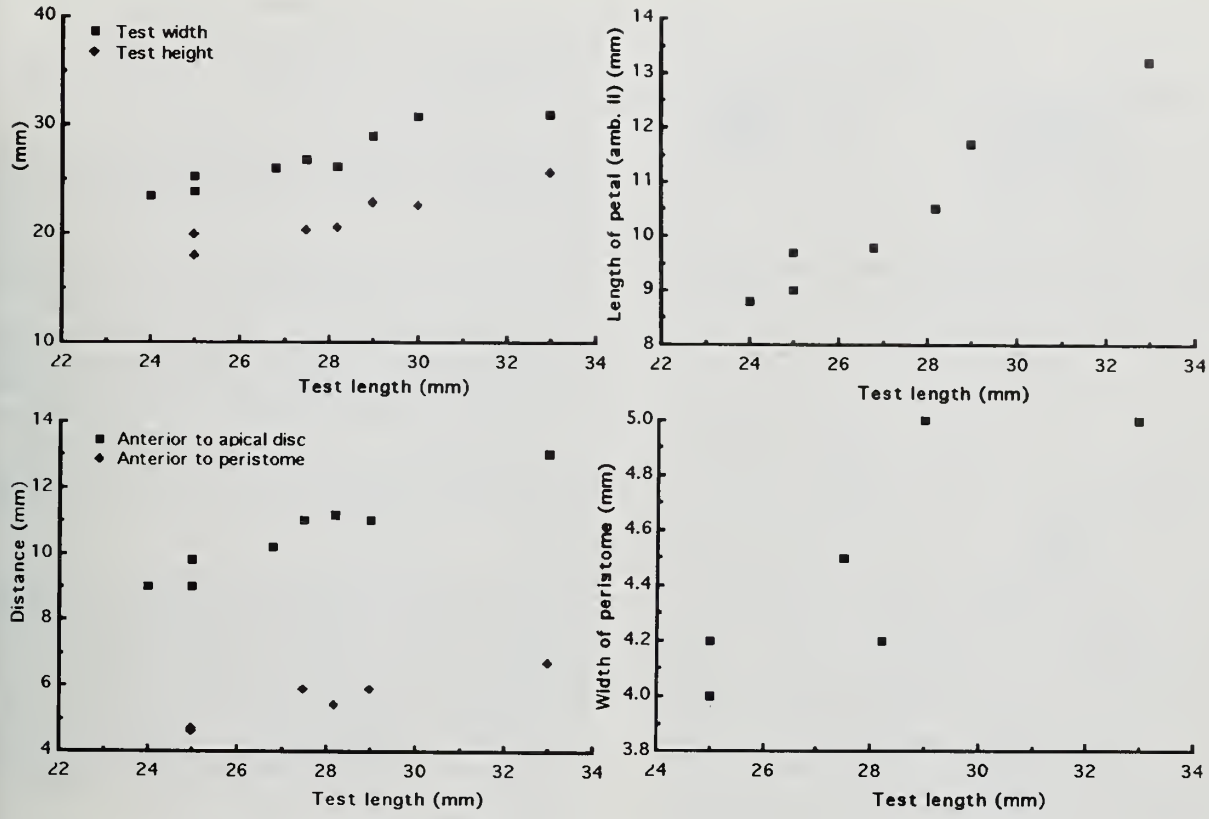


Fig. 82 Biometric data for *Mecaster victoris* (Lambert).

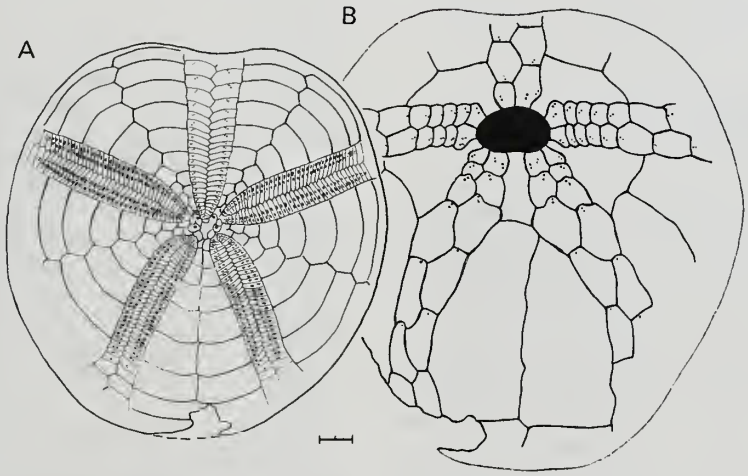


Fig. 83 Camera lucida drawings of plating in *Mecaster victoris* (Lambert). **A**, apical surface, BMNH EE4050; **B**, oral surface, BMNH EE4049. Scale bar = 2 mm.

DESCRIPTION. The specimen is not well preserved but retains sufficient features to be able to place it generically. The test is 32·5 mm in length, 30·5 mm in width (93% of length) and 24 mm in height (74% of length). It is heart-shaped in outline with a squarely truncated posterior and a rather deep anteal sulcus, approximately 2·5 mm deep (7% of test length). The anteal sulcus is relatively broad and deepens gradually away from the apex. In profile the test is rather flat above and below and has a rounded anterior and steep posterior.

The apical disc is ethmolytic and gonopores are large, those on either side almost touching (Fig. 84B). It lies well anterior of the centre, the anterior gonopores being 38% of the test length from the anterior border. The posterior ocular plates are separated by the posteriorly elongated madreporite plate. The antero-lateral ocular plates project and hardly indent the adjacent genital plates.

The anterior sulcus has small isopores that are not crowded together. The anterior petals are 13·5 mm in length and

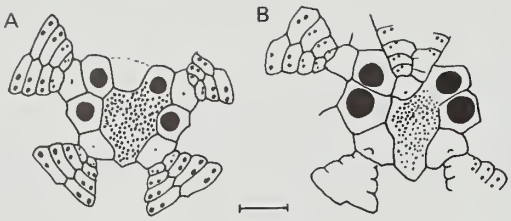


Fig. 84 Camera lucida drawing of apical discs. **A**, *Mecaster victoris* (Lambert), BMNH EE4050. **B**, *?Linthia sudanensis* (Bather), BMNH EE4054. Scale bar = 1 mm.

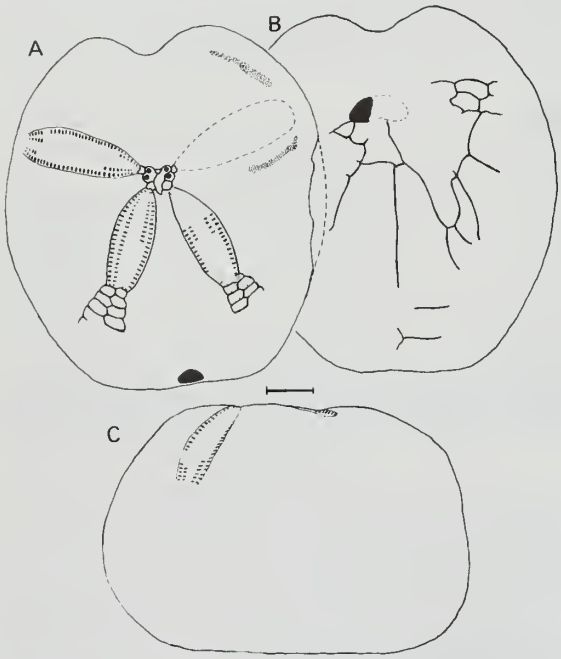


Fig. 85 Camera lucida drawing of *?Linthia sudanensis* (Bather), BMNH EE4054. **A**, apical; **B**, oral; **C**, lateral. Scale bar = 5 mm.

widely divergent (Fig. 85). They extend for most of the distance to the ambitus when viewed from above. Inner and outer pores are equally slit-like and there are 33 pore-pairs in a column. The posterior petals are shorter, only 10 mm in length, and reach approximately half-way towards the ambitus. There are 24 pore-pairs in a column.

The periproct is just visible from above. It is 6·5 mm in height and 4 mm in width, being pointed adapically. The base of the periproct lies just above mid-height, some 11·3 mm above the base of the test (52% of test height).

The plastron is asymmetric, with the median suture displaced towards the right. The labral plate is short (11·5 of the test length) and trapezoidal in outline. The peristome is D-shaped although the labral plate does not project over the peristome much. The peristome is set rather far back from the anterior border, its anterior margin being 23% of the test length from the anterior.

REMARKS. The specimen is unfortunately very badly preserved and cannot be identified to species level with any certainty. However, from the general shape and petal form it cannot be distinguished from the common Palaeocene species *Linthia sudanensis* described by Bather (1904) from Sudan.

Genus ***PRORASTER*** Lambert, 1895

Proraster geayi Cottreau, 1908 Pl. 34, figs 1–3, 8

1908 *Proraster Geayi* Cottreau: 26, pl. 4, fig. 5.

TYPES. The syntypes of *P. geayi* are the two specimens described from Marohita, eastern Madagascar by Cottreau (1908) stated to be in the Museum d'Histoire Naturelle, Paris.

MATERIAL STUDIED. Six specimens, BMNH EE4065–69, EE5037, none of which are particularly well-preserved.

OCCURRENCE. In the western Oman Mountains this species occurs as juveniles in beds 3–5 at Jebel Huwayyah, section 2 (2). Large individuals occur in bed 18 at the top of section 1, Jebel Huwayyah (7), and in bed 9 at Jebel Rawdah, section 1 (2). It is also found in the Maastrichtian of Madagascar.

DIAGNOSIS. A *Proraster* with a very deep anteal sulcus that is closed or almost closed distally by convergence of the lateral walls.

DESCRIPTION. No test is well-preserved, the best specimens being BMNH EE4067 and EE4068. The former is a large individual 71 mm in length, 56 mm in width and about 27 mm in height, whereas the latter is a much smaller individual 27 mm in length, 24 mm in width and 15·6 mm in height. The test is oval in outline with its widest point slightly posterior of midline (Pl. 34, fig. 8). In profile the test is depressed and wedge-shaped, sloping gradually towards the anterior. The posterior is almost vertical and the tallest point on the test lies close to the posterior.

The apical disc lies well towards the posterior, 66–69% of test length from the anterior border. Plating is not seen in any specimen.

The anterior ambulacrum is extremely deep and at the ambitus is about 10% of the test length in depth. The walls are concave with the adjacent interambulacra curving over the groove. Towards the anterior the two sides almost touch so as to roof over the sulcus. The groove thus appears pinched shut close to the anterior (Pl. 34, figs 1, 3, 8).

Petals are sunken. The anterior pair curve forward and run parallel with the anteal sulcus for about two thirds of its length. The posterior petals are very much shorter (about one third of the length of the anterior petals) and diverge strongly at about 120°. There is a well developed peripetalous fasciole developed at the base of the petals, which is presumably continuous, but is not seen other than in small patches because of poor preservation. There is no evidence of a latero-anal fasciole.

The peristome is positioned far forward, lying at the base of the anteal sulcus, and faces anteriorly. The periproct is large and situated high on the posterior face.

REMARKS. Although the Omani specimens to hand are not well-preserved they show sufficient detail to be unambiguously assigned to this species. *P. geayi* was first erected for large individuals from the Maastrichtian of Madagascar by Lambert (1908). Lambert (1905) had previously erected the genus *Proraster* for *Schizaster atavus* (Arnaud) from the Campanian of Charante, France and two Iranian species *Opissaster morgani* (wrongly cited as *O. Douvillei*) and *O. centrosus* Cotteau & Gauthier (1895). The genus was erected to encompass *Schizaster*-like forms lacking a latero-anal fasciole.

The species of Cotteau & Gauthier are unfortunately based

on small individuals and are thus not directly comparable with *P. geayi*. Differences between *P. morgani* and *P. centrosus* seem slight and restudy may prove them synonymous. Because they are small, there is the possibility that they represent juveniles of *P. geayi*. However, this seems unlikely since they have much wider and less pinched anterior sulci than very slightly larger individuals of *P. geayi* found in the lower beds at Jebel Huwayyah. This pinching of the frontal groove, whereby the two sides converge and almost touch near the anterior border, becomes very much more pronounced in the larger individuals higher in the section. This character serves to distinguish *P. geayi* from both *P. atavus*, and an undescribed ?Campanian species from Nafun, Oman. Cotteau & Gauthier's species also have a much less well developed anterior notch and their peristome is standard in orientation rather than being subvertical and directed towards the anterior.

It is noteworthy that at Jebel Huwayyah only small individuals are found in the lower levels, in the *Loftusia* facies, while large individuals are found near the top of the section in carbonate marls representing shelf basinal facies. This could be because the two samples represent different species with consistent morphological differences, or because the smaller individuals are juveniles of the larger, but inhabit a different biotope. Without considerably more and better preserved material it is impossible to determine which is correct. For the present I treat the two forms as juveniles and adults of the same species, partially because the small forms are much closer in appearance to the large forms than they are to, for example, *P. morgani*.

REFERENCES

Agassiz, A. 1863. List of the echinoderms sent to different institutions in exchange for other specimens. *Bulletin of the Museum of Comparative Zoology, Harvard*, **1** (2): 17–28.

Agassiz, L. 1836. Prodrome d'une monographie des Radiaires. *Mémoires de la Société des Sciences naturelles, Neuchâtel*, **1**: 168–199.

—— 1838. *Monographie d'Echinodermes vivans et fossils. Première monographie: Des Salénies*. 32 pp., 5 pls. Neuchâtel.

—— 1840. *Catalogus systematicus ectyporum echinodermatum fossilium musei Neocomiensis*. Petitpierre, Neuchâtel, 20 pp.

—— **& Desor, E.** 1847. Catalogue raisonnée des familles, des genres et des éspeces de la classe des echinodermes. *Annales des Sciences naturelles* **7**: 129–168; **8**: 5–35, 355–380.

Airaghi, C. 1939. Echinidi cretacici e terziari della regione di Orfella e della Sirtica. *Annali del Museo Libico di Storia Naturele*, **1**: 253–286.

Ali, M.S.M. 1989. Late Cretaceous echinoids from Gebel El Rowdah, Hatta area, U.A.E. *Neues Jahrbuch für Geologie, Paläontologie und Mineralogie Abhandlungen*, **177**: 393–412.

—— 1992a. Additional echinoids from the late Maastrichtian (Cretaceous) of Gebel El Rowdah, Oman-United Arab Emirates. *Neues Jahrbuch für Geologie und Paläontologie Monatschefte*, **1992 (2)**: 65–74.

—— 1992b. A new genus and species of regular echinoid from the late Cretaceous of Gebel El Rowdah, Hatta area, Oman-U.A.E. *Journal of Paleontology*, **66**: 693–696.

Amard, B., Collignon, M. & Roman, J. 1981. Etude stratigraphique et paléontologique du Cretacé supérieur et Paléocene du Tinrhert et Tademait-E (Sahara Algerien). *Documentes du Laboratoire géologique du Lyon*, **6**: 15–173.

Archiac, A. d' 1835. Formation cretacé du Sud-Ouest de la France. *Mémoires de la Société géologique de France*, serie 1, **2**: 157–192, pls 11–13.

—— **& Haime, J.** 1853. *Description des animaux fossiles du Groupe nummilitique de l'Inde*. 373 pp., 36 pls. Paris.

Aziz, S.A. & Badve, R.M. 1990. Occurrence of *Hemipneustes* Agassiz (echinoid) from Tiruchirapalli Cretaceous, Tamil Nadu, India. *Journal of the Geological Society of India*, **36**: 326–330.

Bather, F.A. 1904. Eocene echinoids from Sokoto. *Geological Magazine* new series, decade 5, **1**: 292–304.

Birkeland, C. 1989. The influence of echinoderms on coral-reef communities. *Echinoderm Studies*, **3**: 1–79.

Checchia-Rispoli, G. 1914. Sopra alcuni Echinidi del Cretaceo superiore della Tripolitania. *Giornale di Scienze Naturali ed Economiche di Palermo*, **30**: 297–310, pl. 1.

—— 1917. '*Zuffardia*,' nuovo genere di Echinide del Senoniano della Tripolitania raccolti dal cav. Ignazio Sanfilippo. *Rendicoti della Royale Accademia dei Lincei*, series 5a, **26** (9): 492–494.

—— 1921. Fauna del Neocretacio della Tripolitania: Echinidi. *Memorie per servire alla descrizione della Carta geologica d'Italia*, **8** (part 2), 31 pp., 3 pls.

—— 1930. Sul genere '*Noetlingaster*' Vredenburg. *Bollettino del R. Ufficio geologico d'Italia*, **55** (10): 1–24, pls 1–4.

—— 1931a. Sopra alcuni spatangoidi del Maestrichtiano della Tripolitania. *Bollettino del R. Ufficio geologico d'Italia*, **56** (5): 1–14, pl. 1.

—— 1931b. Nuove osservazioni sul genere '*Noetlingaster*' Vredenburg. *Bollettino del R. Ufficio geologico d'Italia*, **56** (11): 1–11, pl. 1.

—— 1932a. Echinidi regolari del Maestrichtiano della Tripolitania. *Bollettino del R. Ufficio geologico d'Italia*, **57** (3): 3–16, pls 1–2.

—— 1932b. Echinidi Cretacei della Tripolitania. *Bollettino del R. Ufficio geologico d'Italia*, **58** (9): 1–14, pls 1–2.

—— 1933. Illustrazione di alcuni echinidi del Maestrichtiano della Tripolitania raccolti da Ignazio Sanfilippo. *Memorie della Societa geologica Italiana*, **1** (8): 1–22, pls 1–2.

Clark, H.L. 1917. Hawaiian and other Pacific Echini, Spatangina. *Memoirs of the Museum of Comparative Zoology, Harvard*, **46**: 81–283.

Claus, C.F.W. 1876–1880. *Grundzuge der Zoologie*. 3rd edition 1254 pp. (1876); 4th edition, volume 2, 522 pp. (1880).

Clegg, E.L.G. 1933. Echinoids from the Persian Gulf. *Memoirs of the Geological Survey of India; Palaeontologia Indica*, (New Series) **22** (1): 35 pp.

Cooke, C.W. 1949. *Pygurostoma pasionensis*, a Cretaceous echinoid from Guatemala. *American Museum Novitates*, **1422**, 1–3.

Cotteau, G. 1862–67. *Paléontologie française; Terrain Cretacé*, **7** *(Echinides)*. V. Masson, Paris. 892 pp., Atlas pls 1007–1204.

—— 1892. Echinides nouveaux ou peu connus, (11e article). *Mémoires de la Société zoologique de France*, **6**, 163–174, pls 20, 21.

—— **& Gauthier, V.** 1895. *Mission scientifique en Perse par J. De Morgan, tome III. Etudes géologiques, partie II -paléontologie; échinides fossiles*. E. Leroux, Paris, 142 pp., 16 pls.

——, **Peron P. & Gauthier, V.** 1881. *Echinides fossiles del'Algerie, Septieme Fascicule, Etage Senonien*. G. Masson, Paris. 198 pp. 20 pls.

Cottreau, J. 1908. Paléontologie de Madagascar VI. Les échinides. *Annales de Paléontologie*, **3**: 145–188, pls 13–17.

Desor, E. 1853. Notice sur les Echinides du Terrain nummilitique des Alpes, avec les diagnosis de plusieurs éspeces et genres nouveaux. *Actes de la Société Helvetiques des Sciences Naturelles*, **38**: 1–12.

—— 1855–57. *Synopsis des Echinides fossiles*. Wiesbaden, Paris, 490 pp., 44 pls.

Devries, A. 1967. Etudes sur des échinides fossiles de Turquie. *Travaux de l'Institut de Geologie et d'Anthropologie Prehistorique de la Faculté des Sciences de Poitiers*, **8**: 163–200, pls 1–6.

Duncan, P.M. 1865. A description of the Echinodermata from the strata on the southeastern coast of Arabia and at Bagh on the Nerbudda, in the collection of the Geological Society. *Quarterly Journal of the Geological Society, London*, **21**: 349–363.

—— 1889. A revision of the genera and great groups of the Echinoidea. *Journal of the Linnean Society (Zoology)*, **23**: 1–311.

Durham, J.W. & Melville, R.V. 1957. A classification of the echinoids. *Journal of Paleontology*, **31**: 242–272.

Ernst, G. 1972. Grundfragen der Stammesgeschichte der irregularen Echiniden der Nordwesteuropäischen Oberkreide. *Geologisches Jahrbuch (A)* **4**: 63–175.

Fell, H.B. & Pawson, D. 1966. Echinacea. *In, Treatise on Invertebrate Paleontology, Part U, Echinodermata 3*, pp. U367–U440. Geological Society of America and University of Kansas Press, Lawrence, Kansas.

Fourtau, R. 1909. Note sur les échinides fossiles recueillis par M. Teilhard de Chardin dans l'Eocene des environs de Minieh. *Bulletin de l'Institut Egyptien*, serie 5, **2**: 122–155.

Gauthier, V. 1889. Description des échinides fossiles recueillis en 1885 et 1880 dans la region Sud des Hauts Plateaux de la Tunisie par Philippe Thomas. *Exploration scientifique de la Tunisie. Illustrations de la partie paléontologique et géologique*. Fascicule 1. pp. 1–116, pls 1–6.

—— 1901. Contribution a l'étude des échinides fossiles, VI. Genre *Noetlingia*, Lambert, 1898. *Bulletin de la Société géologique de France*, 4e serie, **1**: 189–192.

—— 1902. *Mission scientifique en Perse par J. De Morgan, tome III. Etudes géologiques, partie III–échinides supplement*. E. Leroux, Paris, 142 pp., 16 pls.

Geys, J.F. 1985. Regular echinoids from the Cenomanian of Hainaut (Belgium and France). *Bulletin de la Société Belge de Géologie*, **94**: 129–157.

Goldfuss, A. 1829–31. *Divisio secunda; radiariorum reliquae. Petrefacta Germaniae* 1: 115–221, pls 39–45.

Gray, J.E. 1825. An attempt to divide the Echinida, or sea eggs, into natural families. *Annals of Philosophy*, **10**: 423–431.

—— 1835. On the genera distinguishable in *Echinus*. *Proceedings of the Zoological Society, London*, **3**: 57–60.

—— 1851. New genera and species of Scutellidae and Echinolampidae. *Proceedings of the Zoological Society, London*, **19**: 34–38.

Gregory, J.W. 1900. The Echinoidea. *In*, E.R. Lankester (ed.), *A treatise on Zoology. Part III, the Echinodermata*, pp. 282–332. A. & C. Black, London.

Hess, H. 1975. Die fossilen Echinodermaten des Schweizer Juras. *Veröffentlichungen aus dem Naturhistorischen Museum Basel* **8**: 1–130, pls 1–48.

Jensen, M. 1981. Morphology and Classification of Euechinoidea Bronn, 1860; a cladistic analysis. *Videnskabelige Meddelelser fra dansk naturhistorisk Forening i København*, **143**: 7–99.

Kier, P.M. 1962. Revision of the cassiduloid echinoids. *Smithsonian Miscellaneous Collections*, **144** (3): 1–262, pls 1–44.

—— 1966. Cassiduloids. *In*, Moore, R.C. (ed.) *Treatise on Invertebrate Paleontology. Part U. Echinodermata 3*, pp. U492–U523. Geological Society of America and University of Kansas Press, Lawrence, Kansas.

—— 1972. Tertiary and Mesozoic echinoids of Saudi Arabia. *Smithsonian Contributions to Paleobiology*, **10**: 1–242.

—— 1977. The poor fossil record of the regular echinoid. *Paleobiology*, **3**: 168–174.

Krumbeck, L. 1906. Beitrage zür Geologie und Paläontologie von Tripolis. *Palaeontographica*, **53**: 51–136.

Lamarck, J.B. 1816. *Histoire naturelle des animaux sans vertebres, Tome 3 (Echinides)*. Paris, Verdiere, pp. 1–59.

Lambert, J. 1895. Essai d'une monographie du genre *Micraster* et notes sur quelques Echinides. *In*, A. de Grossouvre: Réchérches sur la Craié superièure. Premiére partie: stratigraphie generale, pp. 149–267. *Mémoires pour servir la Carte géologique de France*.

—— 1898. [nomenclatural report]. *Revue critique de Paléozoologie*, **3**: 126.

—— 1900. Etude sur quelques Echinides de l'Infra–Lias et du Lias. *Bulletin de la Société des Sciences historiques et naturelles de l'Yonne*, **53** (2) (for 1899): 3–57.

—— 1903. Note sur quelques nouveaux Echinides cretacés de Madagascar. *Bulletin de la Société géologique de France*, serie 3, **3**: 74–88.

—— 1905. Notes sur quelques Echinides éocéniques de l'Aude et de l'Herault. *In*, L. Doncieux: Catalogue descriptif des fossiles nummulitiques de l'Aude et de l'Herault. Première partie. Montagne Noire et Minervois. *Annales de l'Univiersité de Lyon, nouveaux serie 1, Sciences medecines*, **17**: 129–164.

—— 1906. *In*, Boule, M. & Thevenin, A. Paléontologie de Madagascar. 1, Fossiles de la Côte oriéntale. *Annales de Paléontologie*, **1**: 43–59, pls 1, 2 [Notes on the echinoids by J. Lambert on pp. 52–56].

—— 1911. Description des Echinides cretacés de la Belgique 2. Echinides de l'étage Senonien *Mémoires du Musée Royale d'Histoire Naturelle de Belgique*, **4**: 1–81, pls 1–3.

—— 1916. Sur l'existence de l'etage Valanginien dans l'Aube et dans l'Yonne (avec observations sur les echinides). *Mémoires de la Société Academique de l'Aube*, **80**: 19–94.

—— 1918. Considerations sur la classification des échinides atelostomates. *Mémoires de la Société Academique de l'Aube*, serie 3, **55**: 9–54.

—— 1919. Echinides fossiles des environs de Santander recueillis par M.L. Mengaud. *Annales de la Société Linnéenne de Lyon*, **66**: 1–32.

—— 1927. Revision des Echinides fossiles de la Catalogne *Memorias del Museo de Ciencias Naturales de Barcelona, Serie Geologica*, **1** (1): 1–102, pls 1–4.

—— 1931. Etude sur les Echinides fossiles du Nord de l'Afrique. *Mémoires de la Société géologique de France*, nouveaux serie, **7** (2): 1–108, pls 1–4.

—— 1932. Etude sur les Echinides fossiles du Nord de l'Afrique. *Mémoires de la Société géologique de France*, nouveaux serie, **7** (4): 109–228, pls 5–8.

—— 1933. Echinides de Madagascar communiques par M.H. Besairie. *Annales géologiques du Service des Mines, Madagascar*, **3**: 7–49, pls 1–4.

—— **& Perebaskine, V.** 1930. Note sur quelques échinides du Soudan. *Bulletin de la Société géologique de France*, serie 4, **29**: 471–477.

—— **& Thièry, P.** 1921. *Essai de nomenclature raisonnée des Echinides*. L Ferriere, Chaumont. Pp. 321–384, pl. 9.

—— **& Thièry, P.** 1925. *Essai de nomenclature raisonnée des Echinides*. L Ferriere, Chaumont. Pp. 513–607, pls 12, 13, 15.

Lees, G.M. 1928. Geology and tectonics of Oman and parts of southeastern Arabia. *Quarterly Journal of the Geological Society London*, **84**: 585–670.

Leske, N.G. 1778. *Jacobi Theodori Klein naturalis dispositio. Echinodermatum. Addimenta ad Kleinii dispositionem Echinodermatum*. Lipsis, Officina Gleditschiana. 279 pp., 54 pls.

Loriol, P. de 1897. Notes pour servir a l'étude des Echinodermes. *Revue Suisse de Zoologie*, **5**: 141–178.

Mortensen, T. 1935. *A monograph of the Echinoidea. II, Bothriocidaroida, Melonechinoida, Lepidocentroida and Stirodonta*. C.A. Reitzel, Copenhagen. 647 pp., 89 pls.

—— 1942. New Echinoidea (Camarodonta). *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjobenhaven*, **106**: 225.

—— 1943. *A monograph of the Echinoidea; III 2, Camarodonta, I*. C. A. Reitzel, Copenhagen. 553 pp., 46 pl.

Neraudeau, D. & Moreau, P. 1989. Paléoécologie et paléobiogéographie des faunes d'échinides du Cenomanien nord-Aquitain (Charente-Maritime, France). *Geobios*, **22**: 293–324.

Noetling, F. 1897. Fauna of Baluchistan. Fauna of the Upper Cretaceous (Maestrichtien) beds of the Mari Hills. *Memoirs of the Geological Survey of India. Palaeontologia Indica*, series 16, **1**, part 3, 79 pp. 23 pls.

Orbigny, A. d' 1856. *In* 1854–60. *Paléontologie française. Terrains Cretacés. Tome 6, Echinides*. Mason, Paris. Pp. 1–432, pls 801–908.

Pictet, F. 1857. *Traite de Paléontologie, Tome 4* (3rd edition), xvi + 768 pp., Paris.

Pomel, A. 1883. *Classification méthodique et genera des Echinides vivants et fossiles*. Alger, A. Jourdan. 132 pp., 1 pl.

Roman, J., Roger, J., Platel, J.-P. & Cavelier, C. 1989. Les Echinoides du Cretacé et du Paléogene du Dhofar (Sultanat d'Oman) et les relations êntre les bassins de l'océan Indien et de la Mediterranée. *Bulletin de la Société géologique de France*, Series 8, **5**: 279–286.

Rose, E.P.F. 1976. Some observations on the Recent holectypoid echinoid *Echinoneus cyclostomus* and their palaeoecological significance. *Thalassia Jugoslavica*, **12**: 299–306.

Serra, G. 1934. Osservazioni sull'aparato masticatorio del genere *Orthopsis*. *Rendiconti della Reale Academia (Nazionale) dei Lincei*, series 6, **20**: 50–53.

Skelton, P.W., Nolan, S.C. & Scott, R.W. 1990. The Maastrichtian transgression onto the northwestern flank of the proto-Oman mountains: sequences of rudist-bearing beach to open shelf facies. *In*, Robertson, A.H.F., Searle, M.P. & Ries, A.C. (eds), *The geology and tectonics of the Oman region*. Geological Society Special Publication, number 49: 521–547.

Smith, A.B. 1978. A functional classification of the coronal pores of regular echinoids. *Palaeontology*, **21**: 759–790.

—— 1980. The structure and arrangement of echinoid tubercles. *Philosophical Transactions of the Royal Society, London*, **B289**: 1–54.

—— 1984. *Echinoid Palaeobiology*. Allen & Unwin, London. 199 pp.

—— 1988. Echinoids. *In* Smith, A.B. Paul, C.R.C., Gale, A.S. & Donovan, S.K. Cenomanian and Lower Turonian echinoderms from Wilmington, south-east Devon, England. *Bulletins of the British Museum (Natural History) Geology Series*, **42**: 16–188.

—— **& Bengtson, P.** 1991. Cretaceous echinoids from north-eastern Brazil. *Fossils and Strata*, **31**: 1–88.

—— **& Wright, C.W.** 1989. British Cretaceous echinoids. Part 1, General introduction and Cidaroida. *Monographs of the Palaeontographical Society, London* (Publication number 578, part of volume 141 for 1987), pp. 1–101, pls 1–32.

—— **& Wright, C.W.** 1990. British Cretaceous echinoids. Part 2, Echinothurioida, Diadematoida and Stirodonta (1, Calycina). *Monographs of the Palaeontographical Society, London* (Publication number 583, part of volume 143 for 1989), pp. 101–196, pls 33–72.

—— **& Wright, C.W.** 1993. British Cretaceous echinoids. Part 3, Stirodonta, part 2 (Arbacioida, Hemicidaroida and Phymosomatoida, part 1). *Monographs of the Palaeontographical Society, London* (Publication number 593, part of volume 147 for 1993).

——, **Simmons, M.D. & Racey, A.** 1990. Cenomanian echinoids, larger foraminera and calcareous algae from the Natih Formation, central Oman Mountains. *Cretaceous Research*, **11**: 29–69.

Szorényi, E. 1955. Echinides crétacés de la Bakony. *Geologica Hungarica, Series Palaeontologica*, **26**: 1–332, pls 1–22.

Thum, A.B. & Allen, J.C. 1975. Distribution and abundance of the lamp urchin *Echinolampas crassa* (Bell) 1880 in False Bay, Cape. *Transactions of the royal Society of South Africa*, **41**: 359–373.

Van der Ham, R. 1987. Zeegels uit het Krijt en Tertiair van Maastricht, Luik en Aken. *Publicaties van het Natuurhistorisch Genootschap in Limburg*, **36**: 1–91.

Vidal, L.M. 1921. Contribucion a la paleontologia del Cretacico de Cataluna. *Memorias de la Real Academia de Ciencias y Artes de Barcelona*, **17** (2): 89–107, pls 1–8.

Vredenburg, 1911. Rectification of nomenclature: *Noetlingaster* nom. Mut. *Records of the Geological Survey of India*, **41**: 1.

Zhagbib-Turki, D. 1987. *Les Echinides du Cretacé de Tunisie. Paléontologie générale: systèmique, paléoécologie, paléobiogéographie*. Unpublished thesis of the Faculty of Science, Tunis University.

Bull. nat. Hist. Mus. Lond. (Geol.) **51**(2):241–250 Issued 30 November 1995

Maastrichtian ammonites from the United Arab Emirates-Oman border region

W.J. KENNEDY

Department of Earth Sciences, University of Oxford, Parks Road, Oxford OX1 3PR.

INTRODUCTION

The ammonites described are from the late Cretaceous Qahlah and Simsima Formations of the United Arab Emirates-Oman border region and come from two collections. Some of the specimens were collected by Dr. P.W. Skelton (Open University) in 1990 and are housed in Oxford University Museum (OUM prefixes). The remainder are housed in the Natural History Museum, London (BMNH prefixes) and were mostly collected by A.B. Smith and N.J. Morris during fieldwork in 1991 and 1992. A few specimens were collected by amateur enthusiasts and subsequently donated to the Natural History Museum.

Wherever possible, ammonites have been tied down to specific levels within measured sections. Details of the localities of these sections, and measured lithological logs are given in a preceding section (Smith *et al.*).

SYSTEMATIC DESCRIPTIONS

Order **AMMONOIDEA** Zittel, 1884
Suborder **AMMONITINA** Hyatt, 1889
Superfamily **DESMOCERATACEAE** Zittel, 1895
Family **DESMOCERATIDAE** Zittel, 1895
Subfamily **DESMOCERATINAE** Zittel, 1895
Genus ***DESMOPHYLLITES*** Spath, 1929

(= *Schlüteria* de Grossouvre, 1894: 126 (*non* Fritsch *in* Fritsch & Kafka, 1887: 33); *Schlütericeras* Collignon, 1938: 92 (*non* Hyatt, 1903: 110))

TYPE SPECIES. *Desmoceras larteti* Seunes, 1892: 19, pl. 12 (3), fig. 2; pl. 13 (4), figs 2, 3, by subsequent designation by Spath 1921: 46, as type species of *Schlüteria* de Grossourvre, of which *Desmophyllites* is the replacement name.

Desmophyllites diphylloides (Forbes, 1846) Plate 1, figs 1, 2

1846 *Ammonites diphylloides* Forbes: 105, pl. 8, fig. 8.
1992 *Desmophyllites diphylloides* (Forbes); Kennedy & Henderson: 405, pl. 6, figs 1–9; pl. 16, figs 1–3, 7–8; pl. 17, figs 4–7; fig. 3F (with full synonymy).
1993a *Desmophyllites diphylloides* (Forbes); Kennedy & Cobban: 120, pl. 1, figs 1–8; text-fig. 5c.

TYPES. Lectotype, by the subsequent designation of Matsumoto & Obata (1955: 122) is BMNH C22682, the original of Forbes 1846: pl. 8, fig. 8; paralectotypes are BMNH C22683–85, all from the Upper Maastrichtian Valudavur Formation of Pondicherry, southern India.

DESCRIPTION. BMNH C93992 consists of 270° of body chamber and the nucleus of an individual with an estimated original diameter of 62 mm. Coiling is very involute, with a tiny, pitlike umbilicus, the umbilical wall subvertical and narrowly rounded. The whorl section is compressed, with whorl breadth to height ratio 0·71, the greatest breadth around mid-flank, the flanks feebly convex and subparallel, and the ventrolateral shoulders and venter evenly rounded. The surface of replaced shell and internal mould are smooth, but for a single constriction approximately 70° from the aperture. This is narrow, shallow and markedly prorsiradiate, straight on the inner flank, feebly convex on the outer flank and concave on the outermost flank. Sutures not seen.

DISCUSSION. The types of *Desmophyllites diphylloides* are all rather small (Kennedy & Henderson 1992, pl. 6, figs 1–9; pl. 16, figs 1–3, 7, 8), but Henderson and McNamara (1985: 54, pl. 4, figs 1–4) described larger specimens comparable to the present individual from the Upper Maastrichtian of Western Australia. These show constrictions that are flexuous on the flanks, as with the present material. The other Maastrichtian *Desmophyllites* is *D. larteti* (Seunes, 1892) (p. 19, pl. 12 (3), fig. 2; pl. 13 (4), figs 2, 3; see Hancock & Kennedy 1993: 154, pl. 2, figs 1–3, 10, 11, 14; pl. 3, figs 1, 4, 5), which is a larger, much more compressed species with a narrower, arched venter and much more prominent and markedly flexuous constrictions.

OCCURRENCE. The Oman specimen is from bed 21, Jebel Rawdah, section 2. Elsewhere, the species ranges from Lower Santonian to Upper Maastrichtian. There are records from southern India, Western Australia, Japan; Alaska, British Columbia, California, and Arkansas in the U.S.A.; Argentina, Angola; Pondoland and Zululand (South Africa), Tunisia, and southern France (Corbières).

Family **KOSSMATICERATIDAE** Spath, 1922
Subfamily **KOSSMATICERATINAE** Spath, 1922
Genus ***BRAHMAITES*** Kossmat, 1897

TYPE SPECIES. *Ammonites Brahma* Forbes, 1846: 100, pl. 8, fig. 1, by original designation.

PLATE 1

Figs 1, 2 *Desmophyllites diphylloides* (Forbes, 1846). BMNH C93992, Simsima Formation, Jebel Rawdah, section 2, bed 21.

Figs 3–7 *Pachydiscus (Pachydiscus) neubergicus neubergicus* (Hauer, 1858). **3, 4**, OUM KY 1991, from an unknown level in the Simsima Formation, southern embayment of Jebel Rawdah. **5, 6**, OUM KY 1990, from an unknown level in the Simsima Formation, southern embayment of Jebel Rawdah. **7**, OUM KY 1995, from the basal part of the Simsima Formation, Jebel Huwayyah, close to where the road cuts the north–western part of the outcrop.

All figures are × 1.

Subgenus ***ANABRAHMAITES*** Yabe & Shimizu, 1924
(= *Subbrahmaites* Yabe & Shimizu, 1924: 75).

TYPE SPECIES. *Ammonites vishnu* Forbes, 1846: 100, pl. 7, fig. 9, by original designation.

Brahmaites (Anabrahmaites) vishnu (Forbes, 1846) Pl. 2, figs 9–14

1846 *Ammonites vishnu* Forbes: 100, pl. 7, fig. 9.
1992 *Brahmaites (Anabrahmaites) vishnu* (Forbes); Kennedy & Henderson: 418, pl. 6, figs 25, 26; pl. 9, figs 5–7, 17–20; pl. 10, fig. 5; pl. 17, figs 8, 10–11 (with full synonymy)
1993 *Brahmaites (Anabrahmaites) vishnu* (Forbes); Kennedy & Hancock: 582, pl. 1, figs 5, 6.

TYPES. Lectotype, by the subsequent designation of Kennedy & Henderson (1992: 418), is BMNH C51026, the original of Forbes 1846, pl. 7, fig. 9; BMNH C51027 is a paralectotype. Both are from the Upper Maastrichtian Valudavur Formation of Pondicherry, southern India.

DESCRIPTION. BMNH C93892 (Pl. 2, figs 11–14) consists of 200° of adult phragmocone and body chamber with a maximum preserved diameter of 83 mm, and part of the septate inner whorls, 48 mm diameter. Coiling is very evolute, the shallow umbilicus comprises 55% of diameter, with a broadly rounded umbilical wall and shoulder. The whorl section is depressed reniform, with greatest breadth just outside the umbilical shoulder, and the whorl breadth to height ratio is 1·1. The inner whorls (Pl. 2, figs 13, 14) are badly preserved, but traces of delicate crowded ribs are present on one flank. Both flanks have well-developed, prorsiradiate, deep, narrow constrictions, 2 per half whorl, flanked by a strong adapical collar-rib with feeble umbilical bulla, and a much weaker adapertural rib, the ribs extending across the venter. The outer whorl of the specimen is worn, but shows similar constrictions and collar ribs, with traces of coarse prorsiradiate flank ribs between constrictions. BMNH C93891 is a much larger body chamber fragment (Pl. 2, figs 9, 10), with maximum preserved whorl height 27·7 mm and whorl breadth to height ratio 1·0. There is a single strong constriction, flanked by a bullate adapical collar rib that persists over the venter, where it is strengthened into an incipient bulla (the specimen is worn). There is a much weaker adapertural collar-rib, and blunt non-bullate ribs, straight and prorsiradiate on the flanks, weakened and feebly convex across the venter, cover the remainder of the fragment. Sutures not seen.

DISCUSSION. These fragments are referred to *Anabrahmaites* rather than *Brahmaites sensu stricto* on the basis of the absence of bullae on intermediate ribs and the development of an incipient siphonal bulla. The inner whorls of BMNH C93892 differ in no respects from those of the paralectotype of *B. (A.) vishnu* figured by Kennedy & Henderson (1992, pl. 10, fig. 5); the outer whorls of this specimen and BMNH C93891 also find a match in the Pondicherry material (see also Stoliczka 1865, pl. 79, fig 5).

OCCURRENCE. The Oman specimens are from bed 3 or 4, Jebel Rawdah, section 1. The types are from the Upper Maastrichtian of southern India; the holotype of *Puzosia haugi* Seunes, 1892, a synonym, is from the Upper Maastrichtian *fresvillensis* Zone of southern France. The species also occurs in the Maastrichtian of northern Spain and Armenia.

Family **PACHYDISCIDAE** Spath, 1922
Genus **PACHYDISCUS** Zittel, 1884
Subgenus **PACHYDISCUS** Zittel, 1884

TYPE SPECIES. *Ammonites neubergicus* Hauer, 1858: 12, pl. 2, figs 1–3; pl. 3, figs 1, 2, by the subsequent designation of de Grossouvre 1894: 177.

Pachydiscus (Pachydiscus) dossantoi (Maury, 1930) Pl. 3; Pl. 4, figs 1, 2

1930 *Parapachydiscus dossantoi* Maury: 136, pl. 16, fig. 1; pl. 17, figs 1, 2.
?1944 *Parapachydiscus* sp. Olsson: 107, pl. 16, fig. 1.
1985 *Pachydiscus (Pachydiscus) dossantoi* (Maury, 1930); Zaborski: 20, figs 17, 18, 20.

TYPES. Maury (1930: 136, pl. 16, fig. 1; pl. 17, figs 1, 2) based this species on a number of specimens, referring to an individual 190 mm in diameter as the type. All are from the Maastrichtian on the right bank of Rio Gramame, Fazenda do Congo, Parahyba do Norte, Brazil.

DESCRIPTION. Large, septate to whorl heights of up to 110 mm. Evolute, with 50% of previous whorl covered; umbilicus broad, shallow, with flattened, outward-inclined umbilical wall and broadly rounded umbilical shoulder. Whorl section compressed, with whorl breadth to height ratio of 0·8 in the best-preserved specimen; greatest breadth low on broadly convex flanks; outer flanks convergent; ventrolateral shoulders and venter arched. Coarse, distant ribs arise at blunt umbilical bullae, are straight and prorsiradiate across the flank, alternating regularly with shorter ribs that arise on the outer flank. Ribs sweep forwards across the ventrolateral shoulders and are weakened and broadly convex across the venter. Ornament of this type extends to the end of the phragmocone in BMNH C93895–96 and onto the body chamber in BMNH C93894. Suture poorly preserved (Pl. 3); intricately and deeply subdivided, as is typical for the genus.

DISCUSSION. Compressed whorl section plus persistence of coarse, alternately long and short ribs to a large size show these specimens to belong to *P. (P.) dossantoi*. Of other Maastrichtian species, *P. (P.) neubergicus* (Hauer, 1858) (see revision in Kennedy & Summesberger 1986), *P. (P.) gollevillensis* (d'Orbigny, 1850) (see revision in Kennedy 1986) and *P. (P.) egertoni* (Forbes, 1846) (see revision in Kennedy & Henderson 1992) are also compressed, but all are more delicately ribbed, are mature at smaller diameters, and have adult growth stages characterized by loss of outer flank and ventral ornament. *P. (P.) jacquoti* Seunes, 1890 (see revision in Kennedy 1986) has a depressed whorl section, distant ribs and effacement of outer flank and ventral ornament on the phragmocone.

OCCURRENCE. Most of the Oman specimens come from the lower *Loftusia*-rich beds at Jebel Huwayyah. BMNH C93894 comes from bed 10 or 11, section 1, Jebel Huwayyah, while C93895 comes from bed 10. OUM K1998 (= Skelton 84/32·2) is also from Jebel Huwayyah, section 1, from an unspecified level. One specimen, BMNH C93896, comes from a loose block derived from the basal bed of the Simsima Formation at Jebel Buhays, section 1. The type occurrence is of Maastrich-

tian age, but is difficult to place more precisely within the stage. Kennedy (1986: 44) regarded *Pachydiscus sumneri* Maury, 1930 (p. 155, pl. 13, figs 1, 2), *Parapachydiscus poseidon* Maury, 1930 (p. 155, pl. 15) and *Canadoceras riogramense* Maury, 1930 (p. 169, pl. 21, fig. 2), which are said to occur in the same unit as *P. (P.) dossantoi*, as possible synonyms of the Upper Maastrichtian *Anapachydiscus fresvillensis* (Seunes, 1890). The original figures are so poor, however, and the relative position of species within Maury's 'grey limestone' is unknown, so that only the *possibility* of an Upper Maastrichtian date can be considered. *P. (P.) dossantoi* from Nigeria (Zaborski 1983, 1985) comes from the Nkoporo Shale, and was regarded as 'probably Lower Maastrichtian' (no definition of the Lower/Upper Maastrichtian boundary was given). It co-occurs with *Gaudryceras beantalyense* Collignon, 1956, *Baculites* sp. and *Sphenodiscus lobatus costatus* Zaborski, 1982. On this evidence it can be dated no more precisely than Maastrichtian.

Pachydiscus (Pachydiscus) neubergicus neubergicus (Hauer, 1858) Plate 1, figs 3–7

1858 *Ammonites neubergicus* Hauer: 12 (*pars*), pl. 2, figs 1–3 (*non* pl. 3, figs 1, 2).

1993 *Pachydiscus (Pachydiscus) neubergicus neubergicus* (Hauer, 1858); Hancock & Kennedy: 158, pl. 3, figs 6, 7; pl. 9, figs 5–8; pl. 12, figs 7–9; pl. 13, figs 5–7 (with synonymy).

TYPES. Lectotype, by the subsequent designation of de Grossouvre 1894: 209, is no 1858.01.6 in the collections of the Geologisches Bundesanstalt, Vienna; three paralectotypes bear the same number, and all are from the Lower Maastrichtian of Neuberg, Steiermark, Austria.

DESCRIPTION. The best-preserved specimen is OUM KY 1990 (Pl. 1, figs 5, 6), an internal mould of a phragmocone 93 mm in diameter. Coiling is fairly involute, the umbilicus small, with a flattened, subvertical low wall and narrowly rounded umbilical shoulder. The whorl section is compressed, with a whorl breadth to height ratio of 0·74, the greatest breadth below mid-flank, inner flanks feebly convex, outer flanks flattened and convergent, ventrolateral shoulders broadly rounded, and the venter only feebly convex. There are an estimated 14 umbilical bullae per whorl. These give rise to single ribs, sometimes feebly concave on the innermost flank. They are prorsiradiate and weak across the flanks, where long and short intercalated ribs are inserted, so that there are many more coarse concave ribs at the ventrolateral shoulder, although the number per whorl cannot be determined. OUM KY1994 is a worn but conspecific fragment of phragmocone with a maximum preserved whorl height of 36 mm and whorl breadth to height ratio of approximately 0·89.

OUM K1991–93 are fragments of body chamber (Pl. 1, figs 3, 4), with a maximum preserved whorl height of 51·5 mm and whorl breadth to height ratio of 0·75. At the adapical end of the fragment strong bullate primary ribs at the umbilical shoulder correspond to 3–4 times as many ribs at the ventrolateral shoulder. On the adapical part of the fragment the secondary ribs are lost, and the ornament is of distant primaries that efface across the flanks. OUM K1995 (Pl. 1, fig. 7) is a very worn individual 150 mm in diameter, probably adult, with a phragmocone diameter of 110 mm and whorl breadth to height ratio of 0·78. There appear to be 14–16 primary ribs per whorl, and more numerous primary plus secondary ribs at the ventrolateral shoulder. Sutures not seen.

DISCUSSION. Coiling, whorl proportions and ribbing show these specimens to belong to the *Pachydiscus (P.) neubergicus neubergicus* (Hauer, 1858) – *P. (P.) gollevillensis* (d'Orbigny, 1850) group. Topotypes of the former generally have 14–17 umbilical bullae and 58–60 ventral ribs per whorl (Kennedy & Summesberger 1986), the latter 9–11 umbilical bullae and approximately 80 ventral ribs (Kennedy, 1986), suggesting the present material belongs to the former. Nuclei of *P. (P.) neubergicus neubergicus* and *P. (P.) neubergicus dissitus* Henderson & McNamara, 1985, are identical, but the latter has a mature ornament with many ventral ribs (Henderson & McNamara 1985, pl. 7, fig. 7), not seen in the present material (Pl. 1, figs 3, 4), which are thus referred to the nominate subspecies.

OCCURRENCE. OUM KY1990, 1991–93 (1 specimen) and KY 1994 were collected in the southern embayment of Jebel Rawdah. Their position in the succession is unknown. KY1995 comes from the lower part of the Simsima formation in the north-western part of Jebel Huwayyah, close to where the road cuts the outcrop. Elsewhere the species first appears low in the Lower Maastrichtian, and is best known from the Lower Maastrichtian of Austria, Poland, Ukraine, Armenia, Russia, SW France, northern Spain, Nigeria, Brazil and Zululand (South Africa). It occurs in the lower Upper Maastrichtian of Denmark, and the Upper Maastrichtian of southern India.

Indeterminate pachydiscid

DISCUSSION. BMNH C93987 is a fragmentary pachydiscid, still septate at a whorl height of 150 mm. It bears distant primary ribs, but is indeterminate even as to genus.

OCCURRENCE. The specimen comes from the gritty calcareous bed (bed 9), of the Qahlah Formation, immediately

---

PLATE 2

Figs 1–3, 15, 16 *Lewyites ambindense* (Collignon, 1971). **13**, BMNH C93890; from the *Loftusia*-rich beds, Qahlah Formation, Jebel Huwayyah, section 1, bed 10 or 11. **15, 16**, OUM KY1996; from the basal part of the Simsima Formation, north-western Jebel Huwayyah, close to where the road cuts the outcrop.

Figs 4–8 *Nostoceras (Nostoceras) major* Kennedy and Cobban, 1993. **4–6**, BMNH C93994, from beds 10 or 11, Qahlah Formation, Jebel Huwayyah, section 1; **7, 8**, BMNH C93993, Basal Simsima Formation, bed 9, Jebel Bu Milh, section 2.

Figs 9–14 *Brahmaites (Anabrahmaites) vishnu* (Forbes, 1846). **9, 10**, BMNH C93891; **11–14**, BMNH C93892. Both from the Simsima Formation, bed 3 or 4, Jebel Rawdah, section 1.

Figs 17–19 *Libycoceras*? sp., BMNH C93887, from the conglomeratic basal bed of the Simsima Formation, Jebel Buhays, section 2.

Fig 20 *Nostoceras (Nostoceras)* sp., BMNH C93888, from bed 6, Jebel Huwayyah, section 2.

All figures are × 1

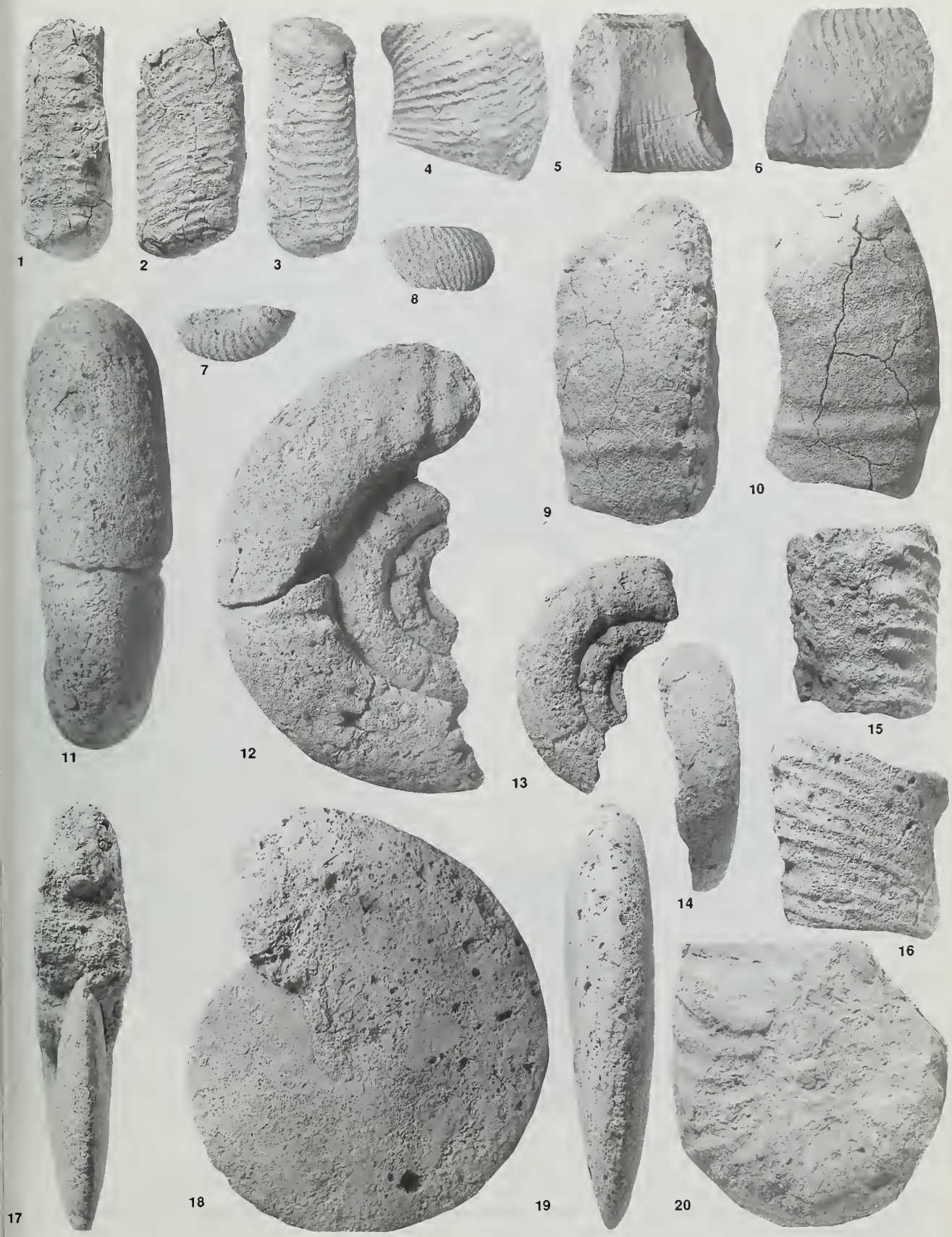

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20

PLATE 3

Pachydiscus (Pachydiscus) dossantoi (Maury, 1930). BMNH C93896, from the basal bed of the Simsima Formation, Jebel Buhays, section 1; slightly reduced.

below the *Loftusia*-rich beds at Jebel Huwayyah, section 1.

Superfamily **ACANTHOCERATACEAE** de Grossouvre, 1894
Family **SPHENODISCIDAE** Hyatt, 1900
(= Libycoceratidae Zaborski, 1982: 306)
Genus ***LIBYCOCERAS*** Hyatt, 1900

TYPE SPECIES. *Sphenodiscus ismaelis* Zittel, 1895, p. 451, text-fig. 631, by original designation.

Libycoceras ? sp. Plate 2, figs 17–19

DESCRIPTION. BMNH C93887 is a very corroded internal mould of a small adult with 240° of body chamber preserved and a maximum diameter of 80 mm. The phragmocone is oxycone, with a whorl breadth to height ratio of 0·4. The body chamber develops subparallel flanks, and the venter rounds progressively; the whorl breadth to height ratio is 0·39 at the aperture. No ornament is preserved on the heavily corroded surface, other than a faint trace of low ribs on the outer flank. The suture (Text-fig. 1) shows a well-developed adventitious lobe in the first lateral saddle, the ventral saddles are feebly indented, and the umbilical saddle is entire.

DISCUSSION. This poorly preserved specimen is referred to *Libycoceras*? rather than *Sphenodiscus* on the basis of its sutural characteristics; it is specifically indeterminate.

OCCURRENCE. BMNH C93887 is from the basal conglomeratic bed of the Simsima Formation at Jebel Buhays, section 2. Species of *Libycoceras* first occur in the Upper Campanian and may range into the Lower Maastrichtian (Zaborski 1982).

Suborder **ANCYLOCERATINA** Wiedmann, 1966
Superfamily **TURRILITACEAE** Gill, 1871
Family **DIPLOMOCERATIDAE** Spath, 1926
(= Neocrioceratinae Spath, 1953)
Subfamily **DIPLOMOCERATINAE** Spath, 1926
(= Scalaritinae Ward, 1976: 455)
Genus ***GLYPTOXOCERAS*** Spath, 1925
(= *Neohamites* Brunnschweiler, 1966)

TYPE SPECIES. *Hamites rugatus* Forbes, 1846: 116, pl. 11, fig. 6, by original designation (Spath 1925: 30, as *Hamites (Anisoceras) rugatus* (Forbes) Kossmat).

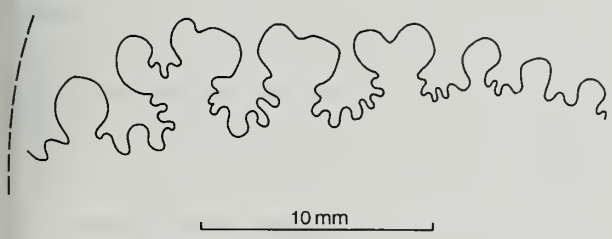


Fig. 1 Idealised suture of *Libycoceras*? sp., based on BMNH C93887, a badly corroded specimen.

Glyptoxoceras sp.

DESCRIPTION AND DISCUSSION. BMNH C93889 is a straight fragment with a whorl height of 6·5 mm, the whorl section is compressed oval, with strong even prorsiradiate flank ribs, transverse on the venter and weakened on the dorsum. It is specifically indeterminate, but ribbing and coiling suggest that it is a *Glyptoxoceras*, a genus recorded from Lower Santonian to Upper Maastrichtian.

OCCURRENCE. BMNH C93889 is from the basal 60 cm shell bed immediately overlying unweathered ophiolite (bed 1) at Jebel Aqabah.

Genus ***LEWYITES*** Matsumoto & Miyauchi, 1984

TYPE SPECIES. *Idiohamites* (?) *oronensis* Lewy, 1969: 127, pl. 3, figs 10, 11, by original designation.

Lewyites ambindense (Collignon, 1971) Plate 2, figs 13, 15, 16

1971 *Neancyloceras ambindense* Collignon: 11, pl. 644, fig. 2380.

TYPE. Holotype, by monotypy, is the original of Collignon 1971, pl. 644, fig. 2380, from the Maastrichtian of locality 504 of Collígnon, Mont Ambinda-Mikoboko (Manera), Madagascar.

DESCRIPTION. BMNH C93890 is a 45 mm long fragment of a straight shaft showing slight curvature at the adapical end. The fragment is wholly septate, with traces of recrystallized shell. The whorl section is compressed oval, with a whorl breadth to height ratio of 0·9 and maximum preserved whorl height of 20 mm. There are 11 ribs in a distance equal to the whorl height. They are narrower than the interspaces, sharp, transverse to feebly convex on the dorsum, sweeping forwards and feebly convex on the dorsolateral margin, markedly prorsiradiate and strengthening across the flank, and transverse on venter. Alternate ribs bear small ventral clavi; occasionaly a second rib is feebly linked to a clavus. Much larger is OUM KY1996, a body chamber fragment with a maximum preserved whorl height of 29 mm. Ornament is as in the smaller specimen, but for the marked effacement of ribs on the dorsum of the internal mould. Sutures not seen.

DISCUSSION. I was unable to trace the holotype of *Neancyloceras ambindense* during a recent examination of the Collignon Collection, housed in the Université de Bourgogne, Dijon. The ribs of the Oman material are more markedly prorsiradiate than in the holotype, with fewer nontuberculate ribs, but they are otherwise similar. Reference to *Lewyites* is based on a comparison with topotypes of the type species in the Oxford University Museum (OUM KY2021–25), and large fragments from New Jersey figured by Cobban (1974, pl. 10, figs 22–35) and Kennedy & Cobban (1993b, figs 5.1–5.18, 5.22–5.26; 7.19, 7.20; 9.4, 9.7).

OCCURRENCE. BMNH C93890 is from bed 10, Jebel Huwayyah, section 1. OUM K1996 (Skelton 84/16·2) comes from the basal part of the Simsima Formation of the northwestern part of Jebel Huwayyah, close to where the section is cut by the road. The holotype is from the so-called Lower Maastrichtian Zone à *Pachydiscus gollevillensis* et *P. neubergicus* of Collignon, but associated ammonites from the type

PLATE 4
Pachydiscus (Pachydiscus) dossantoi (Maury, 1930). BMNH C93895 from the Qahlah Formation, bed 10, Jebel Huwayyah, section 1; × 0·75.

locality in the Collignon Collection indicate Upper Maastrichtian only.

Family **NOSTOCERATIDAE** Hyatt, 1894
(= Jouaniceratidae Wright, 1952: 218; Bostrychoceratinae Spath, 1953: 16;
Emperoceratinae Spath, 1953: 17; Hyphantoceratinae Spath, 1953: 16)
Genus ***NOSTOCERAS*** Hyatt, 1894
Subgenus ***NOSTOCERAS*** Hyatt, 1894

TYPE SPECIES. *Nostoceras stantoni* Hyatt, 1894: 569 (= *Ammonites approximans* Conrad, 1855: 266), by original designation.

Nostoceras (Nostoceras) major Kennedy & Cobban, 1993 Plate 2, figs 4–8

1993c *Nostoceras (Nostoceras) major* Kennedy & Cobban: 6·1, fig. 4.

TYPE. Holotype in Texas Memorial Museum Collections no 77981, from the Upper Maastrichtian Corsicana Formation 1·2 km (0·75 miles) SE of New Sweden, Travis County, Texas.

DESCRIPTION. There are 2 fragments, BMNH C93993, with a whorl height of 13 mm, and BMNH C93994, with a whorl height of 39·5 mm. Both are derived from helices with the whorls in tight contact, there being a shallow concave

impressed zone on the upper whorl face; the outer and lower whorl faces are broadly convex, the inner whorl face is flattened. Ornament is effaced on the impressed zone of the upper whorl face, but wiry narrow ribs strengthen, sweep back and are concave across the juncture of upper and outer whorl faces and are markedly prorsiradiate and narrower than the interspaces on the outer whorl face, sweeping backwards and feebly concave across the juncture of outer and lower whorl faces, straight and prorsiradiate on the lower whorl face and convex and effaced on the inner. All ribs are single on the larger fragment, but occasionally join in pairs at the juncture of outer and lower whorl faces in the smaller fragment. Sutures not seen.

DISCUSSION. The simple coiling and ornament of these fragments occurs in nostoceratids from the Turonian onwards. Given the Maastrichtian age of the specimens, reference to *Nostoceras (Nostoceras)* is indicated. The fragments differ in no significant respect from the holotype of *N. (N.) major*, other than their coiling direction, absence of flared ribs and constrictions, possibly reflecting no more than the short lengths preserved, there being only 2–3 constrictions and associated flared ribs per whorl in the type.

OCCURRENCE. BMNH C93993 comes from bed 9, Jebel Bu Milh, section 2: C93994 comes from bed 10 or 11, Jebel Huwayyah, section 1. The holotype is from the Upper Maastrichtian of Texas.

Nostoceras (Nostoceras) sp. Plate 2, fig. 20

DESCRIPTION AND DISCUSSION. BMNH C93888 is an poorly preserved U-shaped body chamber with a maximum preserved whorl height of 21 mm. Ornament is of coarse single ribs with traces of ventral tubercles on at least some ribs. The specimen is specifically indeterminate, but recalls the *Nostoceras (N.) hyatti* group, of the uppermost Campanian Lower Maastrichtian (Kennedy & Cobban 1993b).

OCCURRENCE. The specimen comes from bed 6, Jebel Huwayyah, section 2.

REFERENCES

Brunnschweiler, R.O. 1966. Upper Cretaceous ammonites from the Carnavon Basin of Western Australia. 1. The heteromorph Lytoceratina. *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics, Australia*, **58**: 58 pp., 8 pls.

Collignon, M. 1938. Ammonites Campaniennes et Maestrichtiens de l'ouest et du sud de Madagascar. *Annales géologiques du Service des Mines de Madagascar*, **9**: 55–118 (1–65), pls 1–9.

—— 1956. Ammonites néocrétaces du Menabe (Madagascar) IV. Les Phylloceratidae. V. Les Gaudryceratidae. VI. Les Tetragonitidae. *Annales géologiques du Service des Mines de Madagascar*, **23**: 1–106, pls 1–11.

—— 1971. *Atlas des fossiles caracteristiques de Madagascar (Ammonites) XVII (Maestrichtien)*. Service Géologique, Tananarive. iv + 44 pp., pls 640–658.

Conrad, T.A. 1855. Descriptions of eighteen new Cretaceous and Tertiary fossils. *Proceedings of the Philadelphia Academy of Natural Sciences*, **7**: 265–268.

Forbes, E. 1846. Report on the Fossil Invertebrata from southern India, collected by Mr. Kaye and Mr. Cunliffe. *Transactions of the Geological Society of London*, (2) **7**: 97–174, pls 7–19.

Fritsch, A. & Kafka, J. 1887. *Die Crustaceen der böhmischen kreideformationen*. Selbstverlag, Prague. 53 pp.

Gill, T. 1871. Arrangement of the Families of Mollusks. *Smithsonian Miscellaneous Collections*, **227**: xvi + 49 pp.

Grossouvre, A. de 1894. Recherches sur la craie supérieure, 2, Paléontologie. Les ammonites de la craie supérieure. *Mémoires du Service de la Carte géologique détaillée de la France*. 264 pp., 39 pls. (mis-dated 1893).

Hancock, J.M. & Kennedy, W.J. 1993. The high Cretaceous ammonite fauna from Tercis, Landes, France. *Bulletin de l'Institut des Sciences Naturelles de Belgique*, **63**: 149–209, 20 pls.

Hauer, F. von 1858. Uber die Cephalopoden aus der Gosauschichten. *Beiträge zür Palaontologie von Osterreich*, **1**: 7–14, pls 2–4.

Henderson, R.A. & McNamara, K.J. 1985. Maastrichtian non-heteromorph ammonites from the Miria Formation, Western Australia. *Palaeontology*, **28**: 35–88, pls 1–9.

Hyatt, A. 1889. Genesis of the Arietidae. *Smithsonian Contributions to Knowledge*, **673**, xi + 239 pp., 14 pls.

—— 1894. Phylogeny of an Acquired Characteristic. *Proceedings of the American Philosophical Society*, **32**: 349–647, pls 1–14.

—— 1900. Cephalopoda, pp.502–604 *in* ZITTEL, K.A. VON 1896–1900, *Textbook of Palaeontology*, transl. EASTMAN, C.R. Macmillan, London and New York.

—— 1903. Pseudoceratites of the Cretaceous. *United States Geological Survey Monograph*, **44**: 351 pp., 47 pls.

Kennedy, W.J. 1986. The ammonite fauna of the Calcaire à *Baculites* (Upper Maastrichtian) of the Cotentin Peninsula (Manche, France). *Palaeontology*, **29**: 25–83, 6 pls.

—— **& Cobban, W.A.** 1993a. Upper Campanian ammonites from the Ozan-Annona Formation boundary in southwestern Arkansas. *Bulletin of the Geological Society of Denmark*, **40**: 115–148, 8 pls.

—— **& Cobban, W.A.** 1993b. Ammonites from the Saratoga Chalk (Upper Cretaceous) Arkansas. *Journal of Paleontology*, **67**: 404–434.

—— **& Cobban, W.A.** 1993c. Maastrichtian ammonites from the Corsicana Formation in northeast Texas. *Geological Magazine*, **130**: 57–67.

—— **& Hancock, J.M.** 1993. Upper Maastrichtian ammonites from the Marnes de Nay between Gan and Rébénacq (Pyrénées-Atlantiques), France. *Geobios*, **26**: 575–594, 7 pls.

—— **& Henderson, R.A.** 1992. Non-heteromorph ammonites from the Upper Maastrichtian of Pondicherry, South India. *Palaeontology*, **35**: 381–442, 18 pls.

—— **& Summesberger, H.** 1986. Lower Maastrichtian ammonites from Neuberg, Steiermark, Austria. *Beiträge zür Pälaontologie von Osterreich*, **12**: 181–242, 16 pls.

Kossmat, F. 1895–1898. Untersuchungen über die Sudindische Kreideformation. *Beiträge zür Paläontologie Osterreich-Ungarens und des Orients*, **9** (1895): 97–203 (1–107), pls 15–25 (1–11); **11** (1897): 1–46 (108–153), pls 1–8 (12–19); **11** (1898): 89–152 (154–217), pls 14–19 (20–25).

Lewy, Z. 1969. Late Campanian heteromorph ammonites from southern Israel. *Israel Journal of Earth Sciences*, **18**: 109–135, pls 1–4.

Matsumoto, T. & Miyauchi, T. 1984. Some Campanian ammonites from the Soya area. *Palaeontographical Society of Japan Special Paper*, **27**: 33–93, pls 10–31.

—— **& Obata, I.** 1955. Some Upper Cretaceous desmoceratids from Hokkaido and Saghalien. *Memoirs of the Faculty of Science, Kyushu University, Series D, Geology*, **5**: 119–151, pls 24–30.

Maury, C.J. 1930. O Cretaceo da Parahyba do Norte. *Monografias Servico Geologico e Mineralogico do Brasil*. 305 pp.; Album das estampas i–xxiii, 35 pls.

Olsson, A.A. 1944. Contributions to the Paleontology of Northern Peru. VII. The Cretaceous of the Paita Region. *Bulletin of American Paleontology*, **28**: 11–46, pls 1–17.

Orbigny, A.d'. 1850. *Prodrome de Paléontologie stratigraphique universelle des animaux mollusques et rayonnés*. **2**, Masson, Paris. 428 pp.

Seunes, J. 1890. Contributions à l'étude des céphalopodes du Crétacé Supérieur de France. 1. Ammonites du Calcaire à *Baculites* du Cotentin. *Mémoires de la Société Géologique de France. Paléontologie*, **1**, Mémoire 2: 1–7, pls 2–3 (1–2).

—— 1892. Contributions à l'étude des céphalopodes du Crétacé Supérieur de France. 1. Ammonites du Calcaire à *Baculites* du Cotentin (Suite). II. Ammonites du Campanien de la région sous pyrénécnne. Départment de Landes. *Mémoires de la Société Géologique de France; Paléontologie*, **1**, Mémoire 2: 8–22, pls 12–15 (3–6).

Spath, L.F. 1921. On Upper Cretaceous Ammonoidea from Pondoland. *Annals of the Durban Museum*, **3**: 39–56, pls 5–9.

—— 1922. On the Senonian ammonite fauna of Pondoland. *Transactions of the Royal Society of South Africa*, **10**: 113–147, pls 5–9.

—— 1925. On Senonian Ammonoidea from Jamaica. *Geological Magazine*, **62**: 28–32, 1 pl.

—— 1926. On new ammonites from the English Chalk. *Geological Magazine*, **63**: 77–83, table.

—— 1929. Corrections of cephalopod nomenclature. *Naturalist*, **871**: 269–271.

—— 1953. The Upper Cretaceous Cephalopod fauna of Grahamland. *Scientific Reports of the British Antarctic Survey*, **3**, 1–60, pls 1–13.

Stoliczka, F. 1865. The fossil Cephalopoda of the Cretaceous rocks of southern

India. *Palaeontologia Indica, Calcutta*, Series 3, part 9: 143–154, pls 71–80.

Ward, P.D. 1976. Upper Cretaceous Ammonites (Santonian-Campanian) from Orcas Island, Washington. *Journal of Paleontology*, **50**: 454–461, pl.1.

Wiedmann, J. 1966. Stammesgeschichte und System der posttriadischen Ammonoideen; ein Überblick. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **125**: 49–79, pls 1, 2; **127**: 13–81, pls 3–6.

Wright, C.W. 1952. A classification of the Cretaceous Ammonites. *Journal of Paleontology*, **26**: 213–222.

Yabe, H. & Shimizu, S. 1924. A new species of *Brahmaites* from the Upper Cretaceous of S. Saghalien, with some remarks on the genus *Brahmaites*. *Japanese Journal of Geology and Geography*, **76:** 77–80, pl. 13.

Zaborski, P.M.P. 1982. Campanian and Maastrichtian sphenodiscid ammonites from southern Nigeria. *Bulletin of the British Museum (Natural History), Geology*, **36**: 303–332.

—— 1983. Campano-Maastrichtian ammonites, correlation and palaeogeography in Nigeria. *Journal of African Earth Sciences*, **1**: 59–63.

—— 1985. Upper Cretaceous ammonites from the Calabar region, southeast Nigeria. *Bulletin of the British Museum (Natural History), Geology*, **39**: 172.

Zittel, K.A. von 1884. *Handbuch der Palaeontology*. **1**, Abt. 2; Lief 3, Cephalopoda, pp. 329–522. R. Oldenbourg, Munich & Leipzig.

—— 1895. *Grundzüge der Palaeontologie (Palaeozoologie)*. R. Oldenbourg, Munich & Leipzig, vii + 972 pp.

Bull. nat. Hist. Mus. Lond. (Geol.) **51**(2):251–255 Issued 30 November 1995

Maastrichtian nautiloids from the United Arab Emirates-Oman border region

NOEL J. MORRIS

Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD

SYNOPSIS. The two nautiloids *Deltoidonautilus salisfilius* sp. nov. and *Cimomia* aff. *sowerbyana* (d'Orbigny) are described from the Maastrichtian Simsima Formation of the United Arab Emirates and Oman.

INTRODUCTION

Cephalopods form only a tiny percentage of the macrofossils collected from the late Cretaceous of the Emirates-Oman border area. They consist only of ammonites and nautiloids and, in spite of the small numbers, it is apparent that the distribution of the two groups is rather different and may reflect their partial ecological separation.

Two distinct species of nautiloids were collected from a number of the Maastrichtian localities on the Emirates-Oman borders. The possibility that they might have been sexual dimorphs is discounted because there are no features in common between the two. For instance, the change in shape on the final whorl of the smaller species does not occur on the larger species.

The nautiloids contrast with those described by Noetling from the Late Cretaceous of the Mari Hills (Pakistan), where species of *Cimomia* and *Deltoidonautilus* do not seem to occur (Noetling 1897).

There seems to be little change in the relatively low nautiloid diversity after the end of the Cretaceous. The apparent loss of *Cymatoceras* is matched by the increase in the Hercoglossidae, mostly in the form of the new suture-line pattern of *Hercoglossa*. This change in shell architecture could represent a wider range of depth tolerance within the superfamily.

SYSTEMATIC DESCRIPTIONS

Superfamily ***NAUTILOIDEA*** de Blainville, 1824
[Name elevated from family rank, Shimanskiy, 1957]
Family **HERCOGLOSSIDAE** Spath, 1927

The distinction between some of the genera in this family is rather dubious: *Cimomia* and *Deltoidonautilus* in particular seem to overlap. Kummel (1964, K456) suggests that *Cimomia* is 'a morphologically transitional form between *Eutrephoceras* and *Hercoglossa*'. Both *Cimomia* and *Deltoidonautilus*, if indeed they are distinct, seem to foreshadow *Nautilus* itself in their shell morphology.

Genus ***DELTOIDONAUTILUS*** Spath, 1927

TYPE SPECIES. *Nautilus sowerbyi* J. de C. Sowerby, 1843 (see footnote by Kummel, 1964: K456–57), from the Lower Eocene, London Clay.

SYNONYMY. *Deltoidonautilus* may yet prove to be a junior synonym of *Angulithes* de Montfort, 1808, because of the various intrepretations of the type species of *Angulithes*, *Nautilus triangularis* de Montfort, 1802. Kummel accepted the name in 1956 but rejected it as a *nomen dubium* in the *Treatise* (1964). It is not clear in de Montfort's (1808: 8) description, whether the type specimen came from the Lower Kimmeridgian or from the Cenomanian. It is beyond the scope of the present work to establish the type material of this taxon, with the result that Kummel's (1964: K456) later opinion that *Angulithes* should be treated as a *nomen dubium* is followed here.

DESCRIPTION. Characteristically smooth, involute and often compressed with a sub-carinate venter in early to middle growth stages. Suture sinuous and projected forwards on the venter. Distinguished from *Cimomia* by the carinate venter.

RANGE. Upper Cretaceous (Cenomanian) to Oligocene; cosmopolitan.

Deltoidonautilus salisfilius sp. nov. Plate 1, figs 1–3

?1861 *Nautilus rota* Blandford: pl. 25, fig. 2 only.
1928 *Nautilus jordani* Zittel; Lees: 663, pl. 44, fig. 6.

HOLOTYPE. BM C.59590, from the 'Main Gastropod Bed', bed 6, at Jebel Bu Milh (JBM 2), NNW of Al Ain; base of Simsima Formation, Maastrichtian, probably Lower Maastrichtian.

OTHER MATERIAL. Thirteen paratypes from the same locality and horizon, BM C.59591–603, Morris and Smith Collection. Three additional paratypes apparently from the same locality and horizon, G.M.Lees collection (mentioned Lees, 1928), BM C.31034–36. Two specimens from the basal 2 meters of the Simsima Formation at Jebel Faiyah (JF2), U.A.E., BM C.59607–08. ?Lower Maastrichtian, Morris and Smith Collection. One specimen from Jebel Faiyah (JF1b), loose, but probably from the basal Simsima Formation, ?Lower Maastrichtian, Gale, Morris and Smith collection, BM C.59609. One specimen from Jebel Buhays (JB1b) also loose but ?basal Simsima Formation, Gale, Morris and Smith collection, BM C.59610. All the specimens found apparently occur

just above the flooding surface at the base of the Simsima Formation, probably at a similar horizon to *Libycoceras* sp. and *Nostoceras* spp.

DESCRIPTION. Shell rather small, the two near complete specimens from Jebel bu Milh are both approximately 102 mm in diameter. Shell planospiral, smooth, involute, non-umbilicate on outer shell surface; internal mould with a narrow, shallow umbilicus. Compressed, discoidal, sub-oxycone with rounded to subcarinate venter on inner and middle whorls; outer whorl, ie. body-chamber, rounded and much less compressed, occupying approximately one third of the last whorl. Siphuncle well dorsal of centre. Suture with well-rounded but relatively narrow ventral saddle that bends forward towards the aperture in a way that is more prominent in the sub-oxycone stages than in the more rounded whorls where the few final sutures occur; broad, shallow, sub-symmetrical lateral lobe; relatively low, smallish lateral saddle close to the umbilical margin. Sutures show considerable crowding towards the body-chamber in what seems to be a fully grown individual. Siphonal sinus moderate on the penultimate whorl, observed only on specimen BM C.31034.

COMPARISON WITH OTHER SPECIES. *Nautilus fleuriausianus* d'Orbigny (1840: 82, pl. 15) has a rounded venter similar to the body-chamber of the present species, but does not have the earlier, more oxycone stage. It is apparently of Upper Cenomanian age from the 'craie à Caprines' at Ile Madame, Charente, France. It may prove to be a more rounded specimen of the widespread species named *Nautilus triangularis* (de Montfort; d'Orbigny, 1840: pl. 12; ?=*Angulithes triangularis* de Montfort 1808). Two nearly complete specimens from the Cenomanian of Sidmouth (BM C.931), and from the Upper Grey Chalk near Folkestone (BM C.8320), are both carinate and show no sign of change to a round ventered body-chamber at approximately 160 mm and 180 mm diameter respectively. *Nautilus mermeti* Coquand, 1862, from Algeria, may also prove to be a synonym of this Cenomanian species.

Nautilus westphalicus Schlüter, 1876 from the Late Santonian or Lower Campanian Quadraten Kreide from Dulmen in Germany also has a carinate body-chamber. *Nautilus galea* Fritsch, 1872, from the Iserschichten in Bohemia, has a carinate venter on the body chamber, has much broader whorls and apparently has less sinuous sutures.

There may be three separate taxa amongst Blanford's (1861) illustrations of his species *Nautilus rota*: his pl. 24 fig. 3 and pl. 25, fig. 1 clearly belong to *Cymatoceras*, while the smooth internal mould of his pl. 25, fig.2 has the flexed suture typical of *Deltoidonautilus* and could well belong in the present species.

Genus *CIMOMIA* Conrad, 1866

TYPE SPECIES. *Nautilus burtini* Galeotti, 1837, from the Eocene of Belgium (a very similar species to *C. imperialis* (J. Sowerby, 1812)).

Cimomia aff. *sowerbyana* (d'Orbigny, 1840) Plate 1, fig. 4; Plate 2

aff. 1840 *Nautilus sowerbyanus* d'Orbigny: 83, pl. 16.
aff. 1850 *Nautilus sowerbyanus* d'Orbigny; d'Orbigny: 189.
1902 *Nautilus jordani* Wanner: 143, pl. 19, fig. 21.
1956 *Cimomia jordani* (Wanner); Kummel: 451.

MATERIAL. A single fairly well-preserved specimen, BM C.59611, from the base of the Simsima Formation at Jebel Fayah (JF 2), associated with *Deltoidonautilus salisfilius* sp. nov.; the body chamber is missing. A single poorly preserved but virtually complete specimen from Jebel Buhays (JB 1b), also apparently from the base of the Simsima Formation, BM C.59612. Three doubtful specimens from Jebel Rawdah (JH 1), one of them *in situ* in the base of bed 5, BM C.59613, and the other two loose on the scree below but apparently from the same horizon, BM C.59614–15.

In his original description, d'Orbigny stated that the locality of the type specimen of *Nautilus sowerbyanus* was unknown, but later, in the *Prodrome* (d'Orbigny, 1850: 189), he gave the locality as Montrichard, France. The specimen was in the Musée d'Histoire Naturelle, Paris, the locality details having been sent by M. Cordier, and it seems quite likely that Fischer, who organised d'Orbigny's collection, must have sorted out the locality before publication of the *Prodrome*.

Wanner's holotype of *Nautilus jordani* came from the uppermost white chalk near Bab-el-Jasmund to the north of Dachel, western Egypt.

DESCRIPTION. Shell medium-sized, planospiral, smooth, involute. External shell non-umbilicate, with the umbilicus of the internal mould plugged by a slight recurved extension of the lateral saddle, almost in the form of a small very shallow lobe. Shell inflated to spheroidal with flanks converging to the rounded but slightly flattened venter. Suture with a very low, gently rounded ventral saddle, a symmetrical, relatively shallow lateral lobe and a relatively prominent well-rounded lateral saddle.

COMPARISON WITH OTHER SPECIES. ?*Cimomia applanatus* (Wanner, 1902: 143), another species named from western Egypt, could be another variant of this species but is considerably more evolute than any of the specimens considered here from the same area. The identification of *Nautilus desertorum* Quaas (1902: 299) is also uncertain, because it is not possible to judge from the original illustration whether the suture-line is sinuous like that of *Cimomia* or straighter like that of *Eutrephoceras*.

Cimomia aff. *sowerbyana* is similar in general shape to *Nautilus sublaevigatus* d'Orbigny (1850: 189; *nom. nov.* for *N. laevigatus* d'Orbigny, 1840: pl. 17, *non* Reinecke, 1818). The first locality listed where d'Orbigny collected this species is Martrou near Rochefort. He also listed a number of other localities including Montrichard, Uchaux and several from Cotentin; these span a range from Turonian to Maastrichtian. The sutures of *N. sublaevigatus* seem much less sinuous than those of *Cimomia sowerbyana* and suggest that this species

PLATE 1

Figs 1–3 *Deltoidonautilus salisfilius* sp. nov. Base of Simsima Formation Maastrichtian, ? Lower Maastrichtian, Jebel Bu Mil;ch, NNW of Al Ain. **1**, holotype, BM C.59590; **2**, paratype, BM C.59591; **3**, paratype, BM C.59592, arrow shows poistion of the siphuncle; all × 1.

Fig. 4 *Cimomia aff. sowerbyana* (d'Orbigny, 1840). Base of Simsima Formation, ?Lower Maastrichtian, Jebel Fayah, south of Dayid, ventral view; BM C.59611; × 1.


1a
1b
2a
2b
2c
4
3

PLATE 2
Cimomia aff. sowerbyana (d'Orbigny, 1840). Base of Simsima Formation, (?Lower) Maastrichtian, Jebel Fayah, south of Dayid; BM C.59611; **1a**, side view; **1b**, apertural view; arrow shows the position of the siphuncle; × 0·75.

belongs to *Eutrephoceras*. Similarly *N. vastus* Kner, 1850, *Cimomia* cf. *forbesi* d'Archiac & Haime, 1854 (a Danian species), and *Eutrephoceras sphaericus* (Forbes, 1846) (holotype from Pondicherry, India, BM C.73524; not pre-occupied by *Nautilites sphaericus* Martin, 1809), may belong to *Eutrephoceras*.

A number of Late Cretaceous specimens in the BM(NH) collection from the United States also indicate that *Nautilus dekayi* Morton, 1833, does not have the sinuous suture-line of *Cimomia* and properly belongs in *Eutrephoceras*.

REFERENCES

Blainville, H. M. D. de 1824. *Dictionaire des science naturelles; Mollusques*, **32**: 392 pp. Strasbourg and Paris.

Blandford, H. F. 1861. The Fossil Cephalopods of the Cretaceous rocks of Southern India, (Belemnitidae - Nautilidae). *Memoirs of the Geological Survey of India, Palaeontologia Indica*, **1**: 40pp., 25pls.

Conrad, T. A. 1866. Observations on Recent and fossil shells, with proposed new genera and species. *American Journal of Conchology*, **2**: 101–03.

Coquand, M. H. 1862. *Géologie et Paléontologie de la région sud de la Province de Constantine*. Marseille.

Forbes, E. 1846. Report on the fossil Invertebrata from southern India collected by Mr. Kaye and Mr. Cunliffe. *Transactions of the Geological Society of London*, (2) **7**: 97–174, pls. 7–19.

Fritsch, A. & Schloenbach, U. 1872. *Cephalopoden der böhmischen Kreideformation*. 52 pp., 16 pls. Prague.

Galeotti, M. H. 1837. Mémoir sur la constitution géognostique de la province de Brabant, en réponse à la question suivante: décrire la constitution géologique de la province de Brabant, déterminer avec soin les éspeces minérales et les fossiles que les divers terrains renferment et indiquer la synonymie des auteurs qui en ont déjà traité. *Mémoires couronnés de l'Académie Royale des Science et Belles Lettres*, **12**: 1–192, pls. 1–4. Bruxelles.

Kner, R. 1850. Versteinerungen des Kreidemergels von Lemberg und seiner Umgebung. *Naturwissenschaftliche Abhandlungen (Haidinger)*, **3** (2): 1–42, pls 1–5.

Kummel, B. 1956. Post-Triassic Nautiloid Genera. *Bulletin of the Museum of Comparative Anatomy at Harvard College*, **114** (7): 321–494, 28 pls.

—— 1964. Nautiloida-Nautilida. *In* **Moore, R.C.** (editor), *Treatise on Invertebrate Paleontology*, **K, Mollusca 3**, 519 pp. The Geological Society of America and the University of Kansas Press.

Lees, G. M. 1928. Geology and tectonics of Oman and parts of southeastern Arabia. *Quarterly Journal of the Geological Society of London*, **84**: 585–670.

Montfort, D. de 1808. *Conchyliologie systématique et classification méthodique des coquilles; offrant leur figures, leur arrangement générique, leurs descriptions caractéristiques, leurs noms; ainsi que leur synonymie en plusieurs langues*. **1**: 409 pp., 100 pls. Paris.

Morton, S. G. 1833. Supplement to the 'Synopsis of the Organic Remains of the Ferruginous Sand Formation of the United States', contained in Vols XVII and XVIII of this Journal. *American Journal of Science*, **23** (2): 288–94.

Noetling, F. 1897. Fauna of Baluchistan, Vol. 3, part I, Fauna of the Upper Cretaceous (Maastrichtian) Beds of the Mari Hill. *Memoirs of the Geological Survey of India, Palaeontologia Indica*, (16) **1** (3): 79 pp., 23 pls.

Orbigny, A. d' 1840. *Paleontologie Française. Terraines Cretacées. Céphalopodes*. **1**: 662 pp., 148 pls.

—— 1850. *Prodrome de Paléontologie stratigraphique universelle des animaux mollusques et rayonnes faisent suite au cours elementaire de Paléontologie*. 3 vols. Masson, Paris.

Quaas, A. 1902. Beitrag zur Kenntniss der Fauna der obersten weissen Kreidebildungen in der libyschen Wüste (Overwegischichten und Blätterthone). *Palaeontographica*, **30** (2) (4): 153–355, pls 20–33.

Schlüter, C. 1876. Cephalopoden der oberen Kreide. *Palaeontographica*, **24** (2): 123–263, pls. 36–55.

Shimanskiy, V. N. 1957. Sistematica i Filogenia otryada Nautilida. *Bulletin de la Societe des Naturalistes de Moscou, Geologie*, **32** (4): 105–20 [In Russian].

Sowerby, J. & Sowerby, J. de C. 1812–1846. *A Mineral Conchology of Great Britain*. **Vols 1–7**, 650 pls.

Wanner, J., 1902. Die Fauna der obersten weissen Kreide der libyschen Wüste. *Palaeontographica*, **30** (2) (3): 91–151, pls 13–19.

Bull. nat. Hist. Mus. Lond. (Geol.) **51**(2):257–265 Issued 30 November 1995

Maastrichtian Inoceramidae from the United Arab Emirates-Oman border region

NOEL J. MORRIS

Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD

SYNOPSIS. Descriptions of Inoceramids from Upper Cretaceous post-Semail Nappe emplacement deposits include *Endocostea (Selenoceramus) semaili* sp. nov. Most specimens are from the Simsima Formation in Jebel Rawdah, immediately below the massive limestone facies, and they indicate a mid-Maastrichtian age.

INTRODUCTION

Small collections of Inoceramidae from two localities on the western edge of the Omani Mountains, close to the border between the United Arab Emirates and Oman, are preserved largely as uncrushed internal moulds. The first is from the Simsima Formation in Jebel Rawdah just north of the Al Ain to Hatta Road, about 10 Km east of the Madam Roundabout, just east of the Omani Border Post, and is of mid-Maastrichtian age. The second is from the *Loftusia*-rich marls below the Simsima Formation in Jebel HuwaYyah (known as Fossil Valley), to the east and north-east of Al Ain, and is apparently of Lower Maastrichtian age. It is quite clear that the specimens from the higher horizon, i.e. in Jebel Rawdah, assist with the age determination of the strata, and they may have potential for international correlation.

The Inoceramidae show that at least three distinct lineages existed in the eastern Arabian area in mid-Maastrichtian times. Each lineage seems to fall in some part of Whitfield's (1877) genus, *Endocostea*, which is in much need of revision. Any serious revision is, however, beyond the scope of this paper. Subgeneric names are used tentatively until we have a better understanding of the phylogeny of the group. The apparent lack of specimens of *Trochoceramus*, which is widespread across Africa in late Campanian and Maastrichtian times, may reflect the palaeoecology. The water may have been either too shallow or too warm, or the sediment too coarse.

The specimens described here were collected by Drs Gale, Morris and Smith in January 1992, by Drs Nolan and Skelton during an earlier visit (Nolan *et al.* 1990), and by members of the Emirates Natural History Group.

Class **BIVALVIA** Linnaeus 1758
Subclass **PTERIOMORPHIA** Beurlen, 1944
[*nom. trans.* Newell, 1965]
Superfamily **INOCERAMOIDEA** Giebel, 1852
[?=Ambonychioidea Miller, 1877]

The Inoceramidae share with *Ambonychia* the thick calcitic inter-umbonal ligament area not present in adult Pterioidea.

Family **INOCERAMIDAE** Giebel, 1852

DESCRIPTION. Variously shaped, concentrically lamellose or plicated or radially plicated *Pteria*-like bivalves which sometimes grew to a large size. The outer calcareous shell layer consists of vertical calcite prisms which are modified to pyriform laths on the ligament area. The ligament, usually multivincular, is attached largely to this external layer; inner shell layer nacreous; usually lacking hinge teeth; usually equivalve or subequivalve, some species inaequivalved. A complex of muscle scars close to the umbones is consistant with byssal fixation. Apparently monomyarian with the posterior adductor often close to the posterior ventral margins but often obscure. It is very difficult to be certain whether an isolated muscle scar situated about halfway below the umbones and towards the anterior margin is a large pedal muscle scar or a small anterior adductor. The Inoceramidae became extinct by the beginning of the Tertiary.

COMMENTS. The ligament area of these later Cretaceous species is seldom well-exposed and the pits characteristic of earlier species have only been observed on one of the species. It remains possible that lineages other than *Tenuipteria* (Dhondt, 1983b) have no pits for the differing ligament types.

THE INTERNAL SHELL RIB. Many post-Coniacian Inoceramidae have an internal shell rib, sillon or Hohlkehle. The nature of this internal rib has been discussed on a number of occasions (especially Seitz, 1967: 14–41). It occurs commonly in a number of Inoceramidae from at least as early as the Santonian. It is here considered to be an architectural character of the shell, and it is clearly variable in some of the taxa that have it. Two specimens of *Endocostea* sp. from the Santonian-Campanian, Haslam Formation of Brannan Creek, Nanaimo District, British Columbia, Canada, demonstrate this point; in BM LL 28194 the inner 'rib' is poorly developed, starting at approximately 6 cm from the umbo of the right valve and continuing for only 2 cm, whereas BM LL 28217, a slightly smaller individual from the same locality and horizon, developed the rib at 1·5 cm from the umbo of the right valve, from which position it continues for at least 4·5 cm towards the posterior ventral margin.

In three well-preserved specimens from the late Campanian, Fort Pierre Group (two examples of '*Inoceramus*' aff. *barabini* Morton, BM L 21569 from the Cheyenne River Section, BM L 7577 from the Powder River Range, Montana, and a single example of '*Inoceramus*' *tenuirostris* Meek &

Hayden, 1862, BM L 21571, from the Cheyenne River), no fully developed internal rib is present. In its place are raised ridges on the innermost shell following the track of the normal position of the inner rib. These end distally as tangents to the 1 cm wide muscle scar that has been referred to as the posterior adductor. Clearly, inoceramids have an unusual arrangement of their soft parts, but it would appear the inner rib is formed as a sensitive emplacement of shell material to enhance strength in the part of the shell under stress from muscular shell closing.

The internal rib is also present on some Jurassic species; a well-preserved specimen of *Parainoceramus ventricosus* (J. de C. Sowerby, 1823) from the Lower Jurassic, Pliensbachian, at Brockthorpe, near Gloucester, shows precisely the same details as '*Inoceramus*' *barabini*, with an internal rib running down to the adductor. Some Campanian specimens of *Endocostea*, however, seem to show the internal rib running very close to the ventral margin, apparently past the position of the adductor.

There are also preservational problems in observing the internal rib. Early diagenesis of the aragonite shell interior can destroy the rib, and there are many examples of inoceramids preserved only as internal moulds of the outer calcitic shell layer.

The rib is nacreous, is often hollow and has an arch-shaped section. In all the examples that I have examined where two valves are preserved together, one rib is an almost perfect mirror image of the other. The rib is in a morphologically comparable position in all species in which it occurs. It shows distinct evolutionary changes, one of the most notable being extreme broadness in some species of *Seleniceramus* (Seitz 1967), though it is usually distinctly narrow. The internal rib may be close to a muscle scar at its distal end.

The claim that the internal rib is formed by, or in response to, a parasite may explain why it is sometimes filled with matrix. This can, however, be equally well explained if it is due to the activity of shell borers: if a hole is bored from the outside of the shell into the hollow of the rib, the damage cannot be repaired by deposition of more shell material as it is separated from the outer surface of the mantle by the thickness of the rib itself. The same would be the case if the inoceramid was already dead when its shell was drilled. All the cases of matrix- filled inner ribs that I have examined show evidence of drilling from the shell exterior.

The inner rib is clearly of some importance for taxonomy at both the species and higher levels. Its variability in some species and its possible diagenetic loss mean that it needs to be used with caution.

Genus *ENDOCOSTEA* Whitfield, 1877

TYPE SPECIES. *E. typica* Whitfield, 1877, by original designation. The lectotype (USNM 12261) was selected by Seitz (1967: 54–55, pl. 2, fig. 4). It is the example 'c' of Whitfield (1880: pl. 9 fig. 3) and is from the Pierre Shale at Old Woman Fork on the Cheyenne River, Black Hills, South Dakota, which is of late Campanian age according to Cobban & Reeside (1952: 1011) (*non Inoceramus cripsi* var. *typica* Zittel, 1866: 98, from the late Cretaceous of Grunbach in Neuen Welt and the Gosau Valley, Austria).

DISCUSSION. The generic name was introduced for relatively small inoceramids with a well-developed inner rib radiating from the umbo towards the posterior ventral margin but stopping well short of that margin. The species is otherwise very similar to Whitfield's own interpretation of *Inoceramus barabini* Morton (Whitfield, 1885: 75–76), except that the latter species apparently does not have the internal rib.

Subgenus *ENDOCOSTEA* Whitfield, 1877

A number of species or subspecies of *Endocostea* are rather convex with prominent or enrolled anterior umbones. These occur in the late Campanian and Maastrichtian and resemble *Endocostea (Endocostea) coxi* (Reyment). They include *Inoceramus balticus pteroides* (Giers, 1964: pl. 1, fig. 6) from the Upper Campanian, Polyplocum Zone of Haldem, Westfalia, and according to Sornay (1976) from Dau, Charente. They possibly also include *Inoceramus borilensis* Jolkicev, said to be from the Maastrichtian in Bulgaria. However, specimens that are very similar to *I. bakalovi* (said by Jolkicev (1961) to occur at the same horizon) occur with ammonites of the Upper Campanian, Donetzianum Horizon, in Nigeria. They also include *Inoceramus impressus* d'Orbigny (lectotype, Museum d'Histoire Naturelle, Paris, 7592a, figured Sornay, 1957: 129) from the ?Upper Campanian of Royan, and '*Inoceramus impressus*' d'Orbigny (*pars*, but not including the lectotype) from the Maastrichtian of Cotentin, Manche, France. These are provisionally included in the subgenus *Endocostea sensu stricto*, although their relationship with the less convex type species remains to be confirmed.

Endocostea (Endocostea) coxi (Reyment, 1958) Plate 1, figs 2–4

1958 *Inoceramus coxi* Reyment: 140, pl. 3, figs 4–6.

MATERIAL. The type material comes from Auchi in north-central Nigeria and is preserved in a medium grained, slightly ferrugenous sandstone (holotype BM L 82963). Some better preserved specimens occur on the Ikot Ekpene Road in the Calabar area associated with magnificent specimens of *Trochoceramus ianjonaensis* and are therefore of 'mid' (probably low Upper) Maastrichtian age. Another specimen in the BM(NH) collection comes from Madagascar. Three specimens were collected by Nolan and Skelton from the south-west face of Jebel Rawdah, BM LL 41647–49.

DESCRIPTION. Convex, equivalved species with strong radiating sulcus posterior to the umbones, delimiting a much less convex posterior area. Somewhat quadrate, but with umbones well to the anterior and prosocline. Strong radiating internal rib well to the posterior of the convex part of the shell. Strong but low rounded comarginal ribs, separated by wider interspaces on anterior and flank, ie. the convex part of the shell, fading posteriorly. Smoother in later growth stages.

COMMENTS. This species was included in *Cordiceramus* by Dhondt (1983a) following Seitz (1967), a genus that was included as a synonym of *Haenleinia* by Cox (1969). *Cordiceramus* Seitz (1961: 110, *ex.* Heinz, 1932) has a very distinctive wide external radiating furrow from the posterior of the umbo to the posterior ventral margin and is more or less equivalve. The type species, *C. cordiformis* Sowerby, is a relatively tall species with a short hinge line, whereas *Haenleinia* is an elongate genus related to *Endocostea*, with a posterior shell twist, resulting in an inequivalve shell in that

PLATE 1 Fig. 1 *Endocostea (Endocostea)* sp. indet.; BM LL 41651, left valve; south-west face of Jebel Rawdah, near base of Simsima Formation, 'mid'-Maastrichtian; Skelton & Nolan Collection, × 2.

Figs 2–4 *Endocostea (Endocostea) coxi* (Reyment). **2**, BM LL 41647, **3**, BM LL 41648, both internal moulds of a right valves; **4**, BM LL 41649; internal mould of a left valve; all from the south-west face of Jebel Rawdah, Nolan and Skelton Collection, × 2.

Figs 5, 6 *Endocostea (Selenoceramus) semaili* sp. nov.; **5**, BM LL 41639, holotype, Jebel Rawdah, section 1, from scree below bed 5, 'mid'-Maastrichtian, Gale, Morris & Smith Collection, × 1; **6**, BM LL 41640, paratype, Jebel Rawdah, section 1, from bed 5, 'mid'-Maastrichtian, Gale, Morris & Smith Collection, × 2.

area. The radiating furrow in some specimens of *E. coxi* is found on composite moulds and reflects its internal rib. Well-preserved specimens of *E. coxi* from near Calabar, Nigeria, have no external furrow and do not seem properly placed in either *Cordiceramus* or *Haenleinia*.

Very similar specimens occur in the low Upper Maastrichtian part of the St Lucia Formation in South Africa (W.J. Kennedy, personal communication).

Endocostea (Endocostea) sp. indet. Plate 1, fig. 1

1844 *Inoceramus impressus* d'Orbigny (pars): 515–16, pl. 409.
?1981 *Inoceramus (Endocostea) impressus* d'Orbigny; Tsankov *et al.*: 97, pl. 42, fig. 2.

MATERIAL. A single specimen from the south-western face of Jebel Rawdah, low in the Simsima formation, Skelton and Nolan Collection, BM LL 41651, 'mid'-Maastrichtian.

THE TYPE MATERIAL OF *INOCERAMUS IMPRESSUS*. Sornay (1957) chose the specimen from Royan in the d'Orbigny Collection as lectotype. This seems to have a much more prominent umbo than the present species, more closely resembling *E. borilensis* Jolkicev and *E. coxi* Reyment. The specimen here (Plate 1, fig 1) although not well preserved, is much more like the species from Cotentin that resembles the left valve only of d'Orbigny's figure. Specimens from the Maastrichtian of Cotentin in the de Gerville Collection in The Natural History Museum, resembling the right valve in d'Orbigny's figure, seem more closely related to *E. coxi* and are mentioned under *Endocostea (Endocostea)* above.

DESCRIPTION. Small elongate species with internal rib. Umbones well to the anterior but not prominent and incurled like the contempory species *E. coxi*. By means of this character, specimens from the Upper Maastrichtian of Cotentin are easily separable from *E. coxi*, although in d'Orbigny's description the species was described as inaequivalve. It seems that he considered that specimens with very prominent umbones, here thought to be related to *E. coxi*, were right valves of the species described here. The species also seems to occur commonly in the Maastrichtian rocks of the St. Lucia Formation from Zululand (W.J.Kennedy Collection).

Subgenus ***SELENOCERAMUS*** Seitz, 1967 (*ex.* Heinz, 1932)

TYPE SPECIES. *Inoceramus (Selenoceramus) selenae* Seitz, 1967, p. 95, by original designation.

Heinz's definition of *Selenoceramus* does not contain characters that distinguish this genus from others, except in his description of the two new species included in the genus. His type species, *Selenoceramus pulcher*, is treated by Seitz (1967: 94), somewhat dubiously, as a *nomen nudum*, apparently because there was no stated type specimen. Seitz attempted to validate the genus in terms of Heinz's original intention. Because of the ambiguity in ICZN article 13(a), it may prove necessary to apply to the International Commission to determine whether the genus should date from Heinz (1932) or Seitz (1967).

COMMENTS. *Selenoceramus* includes some rather small rounded inoceramids with concentric sculpture that show a marked change in growth direction following an evenly curved young stage and have a wide internal rib. The material from the Omani Mountain area shows that this subgenus continues well into the Maastrichtian.

Endocostea (Selenoceramus) semaili sp. nov. Plate 1, figs 5, 6

?1865 *Inoceramus cripsi* Mant, var. *regularis* d'Orbigny; Zittel: 93–99, pl. 14, fig. 3 only.
?1974 *Inoceramus regularis* d'Orbigny; Blank *et al.*: 85, pl. 21, fig. 2; pl. 23, fig. 1.

HOLOTYPE. BM LL 41639, from scree below bed 5, Simsima Formation, Maastrichtian; Jebel Rawdah, section 1; Gale, Morris and Smith Collection.

OTHER MATERIAL. Two small paratypes, BM LL 41640–41, from the same horizon and locality as the holotype; Gale Morris and Smith Collection. Three further paratypes, BM LL 41642–44, from the south-western outcrop in Jebel Rawdah, apparently from the same horizon; Nolan and Skelton Collection.

AGE. The accompanying ammonites and other species of Inoceramidae suggest that this species is of low Upper Maastrichtian age.

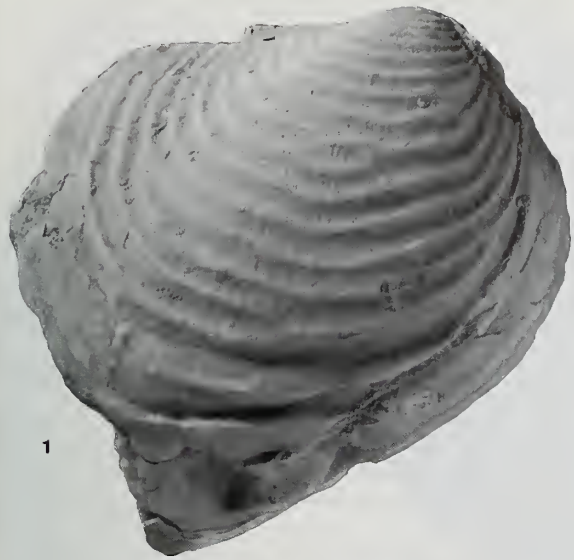
DESCRIPTION. Medium-sized inoceramids with close, regular, rounded, concentric ribs (which show a tendency to straighten) parallel to the anterior-ventral margin. Ribs approach dorsal margin at a relatively high angle to the posterior of the umbones. Maximum shell height below posterior point of hinge. Umbones orthocline, towards but not at anterior. Shells gently convex to a shell height of 70 mm in holotype, then a sharp change of direction to give increased width. This change of shell curvature is at variable distance from the umbones and occurs at an earlier growth stage in two of the paratypes.

The inner rib is angled at about 45° to the hinge line, and is only represented by a trace in the holotype. Two of the paratypes (LL 41642, 43) have a poorly preserved but distinctively wide and shallow internal rib, typical of the subgenus *Selenoceramus*.

The convexity and style of ribbing of *E. semaili* matches that of *E.* cf. *semaili* (Fig. 1) from the Lower Maastrichtian, *Acanthoscaphites tridens* Zone, at Nagoryani, Ukraine, except that it is smaller and the ribbing is consequently closer. However, approximately the same number of ribs are present. Unfortunately, specimens from Nagoryani are not well-preserved on the inner shell surface, making it very difficult to interpret the form of their interior ribs.

The species should be compared with *Endocostea mandembataensis* (Sornay, 1973: 90–91, pl. 4, fig. 4; Fig. 4) from Mandembata, southern Madagascar, 'Lower and Middle' Maastrichtian. Unfortunately, this species is defined on a single rather incomplete figured specimen. The anterior portion of the shell, a left valve, is missing, which does not allow identification at the species level. This species is a *nomen dubium* until further material from the type locality is described. Sornay himself (1973: 11) stated that the material was not sufficiently well preserved to enable him to work out its relationships.

Endocostea semaili should also be compared with *Endocostea kneri* Boehm (1909: 53; *nom. nov.* for *Inoceramus impressus* Kner, 1850, *non* d'Orbigny) from Nagoryani, Ukraine, presumably from the Lower Maastrichtian 'Tridens



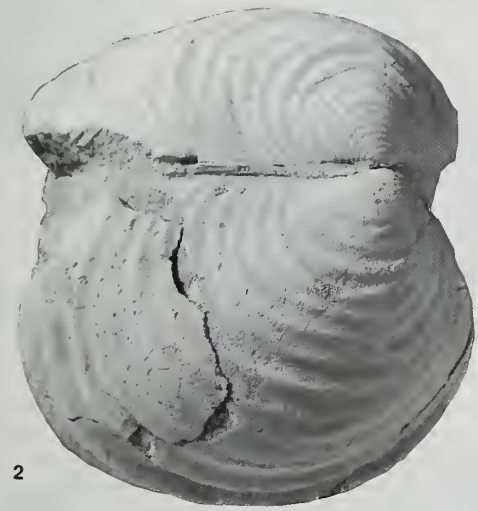


Fig. 1 *Endocostea (Selenoceramus)* cf. *semaili* sp. nov; 'Tridens' Zone, Lower Maastrichtian, Nagoryani, Ukraine; right valve; M. Mackay Collection, BM LL 41653, × 0·5.

Fig. 2 *Endocostea ?(Cataceramus)* sp. indet.; 'Tridens' Zone, Lower Maastrichtian, Nagoryani; M. Mackay Collection, BM LL 41654, × 0·5.

Zone'. When compared with sixteen specimens from Nagoryani in the collections of The Natural History Museum, it is fairly certain that the type of this nominal species is badly distorted. It has become much more elongated than all of them except one. The latter specimen, BM LL 61647, has a normal, rather rounded, right valve, but diagenetic distortion has decreased the height of the left valve. The similarity of the form of the sculpture of this left valve with that of Kner's figure suggests that his specimen was also similarly distorted. For this reason I consider that *Endocostea kneri* is a *nomen dubium* until such a time as its true shape can be described, possibly when the Inoceramidae from Nagoryani are revised. Specimens from Nagoryani are illustrated in Figs 1 and 2.

Endocostea semaili sp. nov. is very similar to *E. (Cataceramus) baltica* (Boehm, 1909; see Geirs, 1964: pl. 1, fig. 1 only) from the late Santonian (? and Lower Campanian) of Germany, but it differs in having the umbones slightly more posterior. Also the comarginal ribs are much more regularly curved in Boehm's species, giving it a very rounded appearance, whereas there is a slight straightening of the ribs ventral to the umbones in *E. semaili*. The nature of the internal rib of *E. (Cataceramus) baltica* is in doubt.

Inoceramus sornayi Dhondt (1993) was a *nom. nov.* for *Inoceramus regularis* d'Orbigny, 1846, *non* Munster, 1840; the lectotype was designated by Sornay (1962), and other specimens were figured by him (Sornay, 1976: pl. 2, figs 3, 4; pl. 3, fig. 4). *I. sornayi* is from the late Campanian and has a wide internal rib, and like *Endocosta semaili*, is better placed in *Selenoceramus*.

E. (Selenoceramus) semaili has its umbones further from the anterior margin than *E. (S.) sornayi* and has a differently shaped anterior; its anterior ventral margin has a diagonally cut away appearance in contrast to the rounded anterior of *E. sornayi* (see Sornay, 1962: pl.7, fig. 3, the lectotype; and Dhondt, 1993: pl.6, fig. 3). *E. (S.) semaili* may have been a descendant and chronological subspecies of *E. (S.) sornayi*. It has not been found amongst the many Inoceramids in the St. Lucia Formation in South Africa, possibly because it is restricted to more northerly areas.

Subgenus *CATACERAMUS* Cox, 1969 (*ex.* Heinz, 1932 ?*nom. nud.*)

TYPE SPECIES. *Inoceramus goldfussianus* d'Orbigny, 1845, by original designation.

Cox's designation of *Inoceramus goldfussianus* d'Orbigny as the type species is unfortunate because it is not the same as *I. balticus* Boehm as he claimed. More unfortunately, the specimen he figured as *I. balticus* has been separated from the type of that species by Giers, and is in fact the holotype of *I. marki* (Giers).

Heinz (1932: 15) proposed *Cataceramus*, with type species *Inoceramus balticus* Boehm, as a subgenus of *Selenoceramus*. Cox implied that Heinz's description does not fulfill the requirements of Article 13 (a) (i) in that there is no definition, and the name may therefore not be valid from that date. The type species, *I. balticus*, was emended by Giers (1964: 238–39). As pointed out by Dhondt (1993), Cox (1969) wrongly included *I. balticus* as a synonym of *I. goldfussianus*, and therefore changed the nature of the genus. Athough Heinz (1933) went on to use his generic name he still did not include characters that distinguished *Cataceramus* from other genera. Seitz (1967: 49) dismissed *Cataceramus* Heinz, 1932, as a synonym of *Endocostea* Whitfield.

IDENTITY OF THE TYPE SPECIES. *Inoceramus goldfussianus* d'Orbigny, 1845, was unnecessarily emended by Sornay (1957; 1976) to *I. goldfussi*. The species was described from the late Cretaceous of Royan by d'Orbigny, and he included the specimen figured by Goldfuss (1836: 116, pl. 112, fig. 4) as *Inoceramus cripsii* Mantell in his synonymy. Sornay (1957) figured the lectotype (d'Orbigny collection, no. 7593), previously chosen by Heinz, and also some new specimens (Sornay, 1976: pls 4, 5).

COMMENTS. In spite of the difficulties with the identity of the type species, this is the '*Inoceramus balticus*' group of many authors. Although Dhondt (1993) suggested that no close relative of *C. goldfussianus* can be recognised, both the

lectotype and Sornay's, 1976, pl. 4, fig. 2, have a definite indication of an internal rib in addition to a general similarity in shape to *I. balticus*. The clear difference is the more spaced out nature of the ribbing, which at present I regard as only significant at species level. *Endocostea (Cataceramus) goldfussianus* would seem to be of late Campanian age as understood here. Specimens from Celles near Riberac, Dordogne, France, suggest that the species occurs as early as the Vari Zone, Upper Campanian.

Upper Santonian and Lower Campanian species of *Cataceramus* are extensively described and illustrated by Seitz (1967) under the subgenus *Endocostea sensu stricto*. The inner rib of Seitz's *E. baltica baltica* is apparently intermediate in form between *Selenoceramus* and *Endocostea sensu stricto*. Unfortunately, the inner shell layer is not preserved on the lectotype of Böhm's species (Giers, 1964: pl. 1, fig. 2).

A number of additional species of this subgenus recognised in the Upper Campanian and Lower Maastrichtian are in need of further revision, but this is beyond the scope of the present paper. Two subspecies are, however, of stratigraphical value: *Endocostea baltica baltica* Boehm (1907: 113; 1909: pl. 11, fig. 2; emended Giers, 1964: 238–39, pl. 1, figs 2–4) and *E. baltica marki* occur in the Upper Santonian of Dulmen. Giers (1964), however, pointed out that *E. baltica* ranges higher, and he considered the subspecies *E. baltica haldemensis* (Giers 1964: 243–44, pl. 2, fig. 2) from the Polyplocum Zone of Haldem, Lemforde, Westfalia (?*non Inoceramus haldemensis* Heinz, ?*nomen nudum*) to be typical of the Upper Campanian. Two other subspecies, *E. baltica ellipticus* and *E. baltica sublaevigatus*, occur in the low Upper Campanian at Tercis, south-west France (Dhondt, 1993).

Endocostea (?Cataceramus) aff. *goldfussianus* (d'Orbigny, 1846) Plate 2, fig. 4

1846 *Inoceramus goldfussianus* d'Orbigny: 517, pl. 411.
1976 *Inoceramus goldfussi* d'Orbigny; Sornay: 9–11, pl. 4; pl. 5, figs 4, 5.

MATERIAL. A single specimen, kindly donated by Mrs Valerie Chalmers and other members of the UAE Natural History Group, BM LL 41645. Apparently from Jebel Rawdah, its calcarenite matrix is rich in *Lepidorbitolina* sp., and it seems to come from the same horizon as the other material from this locality.

COMMENTS. Whereas this individual might be a variant of *E. (S.) semaili* sp. nov., it has a rather different ribbing pattern, clearly similar to that of the earlier *E. golfussianus* (d'Orbigny), but closer packed. There is a slight change in shell curvature suggesting that it would have been a considerably smaller individual when full grown than the typical late Campanian specimens of western France. It also closely resembles a specimen from the Lower Maastrichtian, 'Tridens Zone', of Nagoryani, Ukraine (Fig. 2).

ENDOCOSTEA BEBAHOAENSIS AND RELATED SPECIES. A number of inflated species of late Campanian and Maastrichtian age seem to form a natural group. They have umbones well to the anterior and show no change of growth direction as they approach full size. They include:

1. *Inoceramus cripsi* Mantell var. *decipiens* Zittel, 1865: 95–99, pl. 15, fig. 1; Gosau Beds, Grunbach, Austria.
2. *Inoceramus bebahoaensis* Sornay, 1973: 89, 90, pl. 3, figs 1, 2, text–fig. 4.
3. *Inoceramus balticus beckumensis* Giers, 1964: pl. 2, fig. 1, from the low Upper Campanian, Beckumer Schichten, near Beckum, Germany.
4. ?*Inoceramus balticus* Boehm, Blank *et al.* 1974: 83, pl. 22, fig. 2.
5. *Inoceramus borilensis dauensis* Sornay, 1976: 5, 6, pl. 1, fig. 3; pl. 2, figs 1, 2.
6. *Endocostea flexibaltica* (Seitz); Dhondt, 1993: pl. 4, fig. 4.
7. ?*Inoceramus borilensis* Jolkicev, 1962: 145, pl. 7.

There is apparently no subgeneric name for this group, but I consider it inadvisable to introduce one here because the full relationships within *Endocostea* are insufficiently understood.

'Endocostea' bebahoaensis (Sornay, 1973) Plate 2, figs 1, 2

1973 *Inoceramus bebahoaensis* Sornay: 89–90, pl. 3, figs 1–2, Fig. 4.

MATERIAL. A single well-preserved specimen from the south–west face of Jebel Rawdah, Nolan and Skelton Collection, BM LL 61646.

MATERIAL FROM OTHER LOCALITIES. A single specimen, BM L 74737, from the Upper Maastrichtian, Calcaire a *Baculites*, Cotentin Peninsula, Normandy, in the de Gerville (ex J. de C. Sowerby) Collection. Other specimens are known from the Maastrichtian of Ianjona and Bebahoa, southern Madagascar (Sornay, 1973), and the St. Lucia Formation, Zululand (W.J.Kennedy Collection, Oxford University Museum).

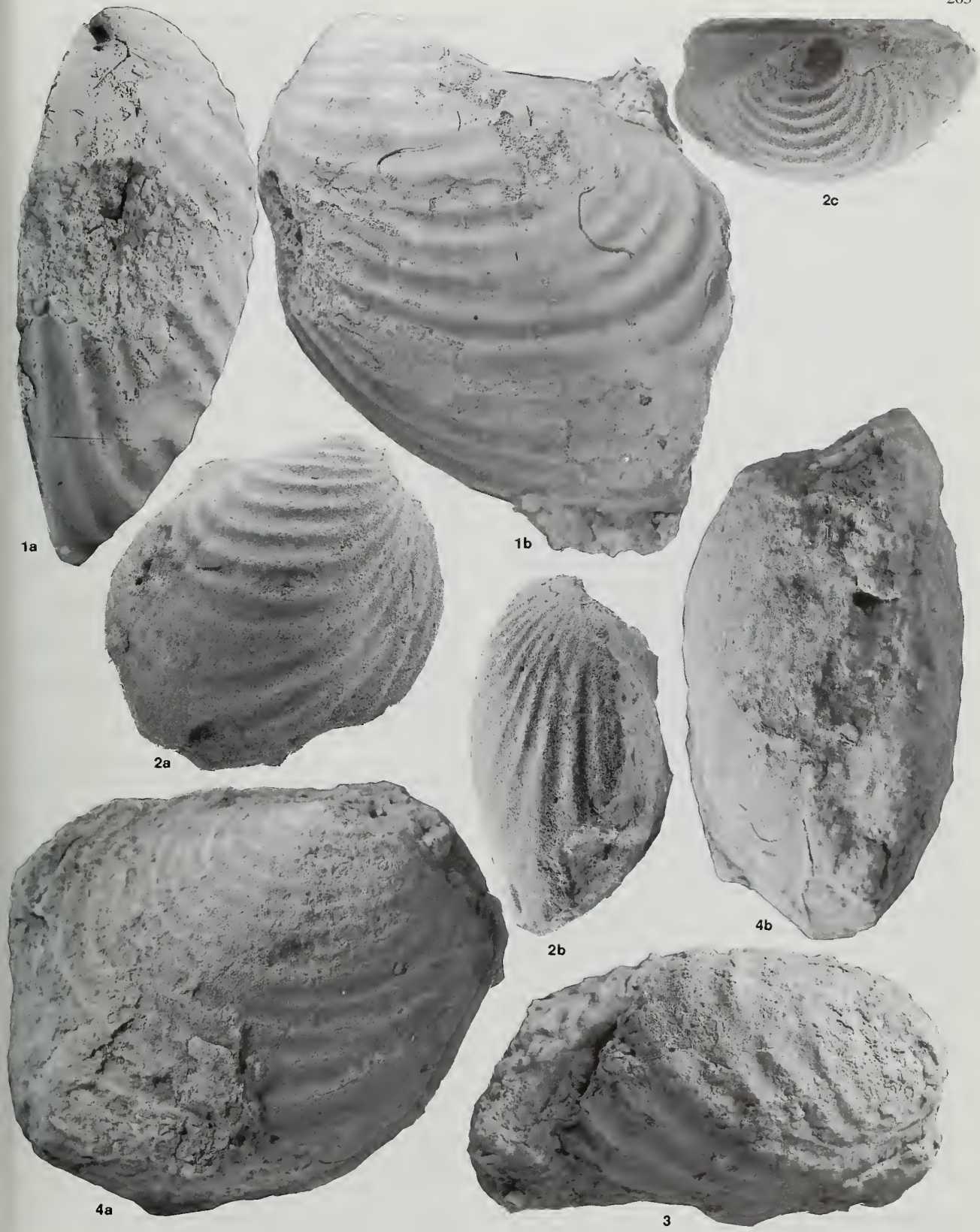
DESCRIPTION. Convex medium-sized species of Inoceramidae with unchanging growth curvature and only gently coarsening, regular, low, rounded, concentric ribs. Umbones well to the anterior and gently prosocline. Our single right valve from Jebel Rawdah is an internal mould and has a shallow narrow groove running from the umbo towards the posterior ventral margin as far as the shell is preserved. This is the impression of the internal rib, which does not seem to have been preserved on other specimens.

PLATE 2

Figs 1, 2 *'Endocostea' bebahoaensis* (Sornay). **1**, BM L 74737, Calcaire à *Baculites*, Upper Maastrichtian, Cotentin Peninsula, France, de Gerville Collection; left valve, 1a, anterior view, 1b, lateral view, × 1. **2**, BM LL 41646, south-west face of Jebel Rawdah, 'mid'-Maastrichtian, near base of Simsima Formation; Nolan & Skelton Collection; right valve, 2a, lateral view, 2b, anterior view, 2c, dorsal view; × 1.

Fig 3 *'Endocostea'* cf. *bebahoaensis* (Sornay). BM LL 41652, *Loftusia*-Beds, Jebel Huwayyah, ?Early Maastrichtian, Gale, Morris & Smith Collection, anterior view of incomplete right valve, × 1.

Fig. 4 *Endocostea (?Cataceramus)* aff. *goldfussianus* d'Orbigny. BM LL 41645, possibly from near the base of the Simsima Formation, Jebel Rawdah. ?Maastrichtian, Mrs. V. Chalmers Collection; 4a, lateral view of right valve, 4b, anterior view, × 1.


1a
1b
2c
2a
2b
4b
4a
3

'Endocostea'* cf. *bebahoaensis (Sornay, 1973). Plate 2, fig. 3

cf. 1973 *Inoceramus bebahoaensis* Sornay: 89–90, pl. 3, figs 1–2, Fig. 4.

MATERIAL AND COMMENTS. A single fragment, BM 41652, from the *Loftusia*-Beds at Jebel Huwayyah, consists of only the anterior portion of the shell. The anterior position of the umbo, the steep drop from the convex flank to the anterior margin and the style of ribbing, demonstrate that this fragment is very similar to *Endocostea bebahoaensis*, particularly the specimen from Cotentin (Plate 2, fig. 1). Ammonite evidence suggests that the Campanian-Maastrictian boundary may lie within the *Loftusia*-Beds, and the occurrence of *Pachydiscus dossantoi* (Maury, 1930) in the upper part of these beds suggests that the age here is at least as high as mid-Maastrichtian.

Genus ***PLATYCERAMUS*** Seitz, 1961, p. 54
(*ex. Platyceramus* Heinz, 1932, p. 10, *nomen nudum)*

TYPE SPECIES. *Inoceramus mantelli* de Mercy, 1877, by original designation.

As originally introduced by Heinz (1932: 10), with the type species designated as 'Genotyp: *Inoceramus mantelli* Merc.', it is difficult to interpret this generic name as anything but a *nomen nudum*, because no description or differentiating characters were given. *Inoceramus mantelli* de Mercy, 1877, is based on a number of hinge and outer shell fragments of large inoceramids from northern France, ranging in age from Turonian to Coniacian and possibly into the Lower Santonian. Many of these fragments are similar to bilaterally symmetrical species of immense proportions, not uncommon in the Chalk of England and northern France, but are otherwise not particularly different from *Inoceramus cuvieri* Parkinson, 1819. On this basis it does not therefore seem necessary to distinguish *Platyceramus* from *Inoceramus sensu stricto*.

In Seitz's (1961: 54) more valid use of *Platyceramus* (as a subgenus of *Inoceramus*), the type species *Inoceramus mantelli* de Mercy, 1877, was interpreted according to Barrois' (1879) description of the species (which was based on ?Coniacian specimens). Barrois' interpretation of *I. mantelli* differs from *I. cuvieri* in having a very much wider umbonal angle, in which respect it resembles the South African Coniacian species '*I' expansus* Baily. It will be necessary to apply to the I.C.Z.N. if this interpretation of *Platyceramus* and its type species is to be accepted.

Seitz had a wide interpretation of the genus and included many flattish, bilaterally symmetrical inoceramids from varying parts of the Upper Cretaceous, eg. *Inoceramus cycloides* Wegner. Similar large, often smoothish, narrow species also occur in the Campanian and Maastrichtian. It is difficult to believe that all these flattish species are correctly assigned to the same clade and some will need different generic names. No attempt to solve this taxonomic problem is attempted here.

Cf. ***Platyceramus*** sp. indet.

MATERIAL. A single fragmentary specimen of an almost smooth, very large species was observed in the main gastropod bed at the base of the Simsima Formation at Jebel Bu Milh, section 2. It showed no other characters. The specimen was not collected, but it indicates the presence of '*Platyceramus*'. This genus is common in the Lower Maastrichtian part of the St. Lucia Formation, South Africa, and although less common in the Upper Maastrichtian part of that formation, the highest *Inoceramus* horizon seems to consist entirely of fragments belonging to '*Platyceramus*'.

REFERENCES

Barrois, C. 1879. Sur quelques espèces nouvelles ou peu connues du terrain crétacé du Nord de la France. *Annales de la Societe géologique du Nord, Lille*, **6**: 449–57, pls 4, 5, 12.

Blank, M.R., Krimholtz, L.R., Naidin, D,C. & Sabiuskaya, O.V. 1974. Atlas of the Upper Cretaceous Fauna of the Don Basin. *Ministerstvo Vischego i Srednego Spechialinogo OBrazovanii USSR, Communarskii Gornometallurgiieskii Institut, Isdatelestvo N.E.D.R.A.* Moscow.

Boehm, J. 1907. Über *Haenleinia* nov. subgen. *Zeitschrift der Deutschen geologischen Gesellschaft, Monatsberichte*, **59**: 317.

—— 1909. Über *Inoceramus cripsi* auctorum. *In* **Schroeder, H. & Boehm, J.**, 1909. Geologie und Paläontologie der subhercynen Kreidemulde. *Abhandlungen der Koniglich Preussischen geologische Landesanstalt, Berlin*, N.F. **56**: 39–58, pls 9–14.

Cobban, W. A. & Reeside, J. B., Jr. 1952. Correlation of the Cretaceous Formations of the Western Interior of the United States. *Bulletin of the Geological Society of America*, **63**: 1011–43.

Cox, L. R. 1969. *In* Moore, R. C. (editor). *Treatise on InverteBrate Paleontology*. Part N, Volume 1, Mollusca 6, Bivalvia. xxxviii + 489 pp. The Geological Society of America and the University of Kansas.

Dhondt, A. V. 1983a. Campanian and Maastrichtian Inoceramids: a review. *Zitteliana*, **10**: 689–701.

—— 1983b. Tegulated Inoceramids and Maastrichtian Biostratigraphy. *Newsletters on Stratigraphy*, **12** (1): 43–53, 5 figs.

—— 1993. Upper Cretaceous bivalves from Tercis, Landes, SW France. *Bulletin van het Koninklijk Belgisch Instituut voor Natuurwetenschappen, Aardwetenschappen*, **63**: 211–59, 7 pls.

Giers, R., 1964. Die Grossfauna der Mukronatenkreide (unteres Obercampan) im Ostlichen Munsterland. *Fortschritte der Geologie von Rheinland und Westfalen, Krefeld*, **7**: 213–94, 3 pls.

Goldfuss, A. 1833–40. *Petrefacta Germaniae*, **2**: 312 pp., pls 72–165. Arnz & Co.

Heinz, R., 1932. Aus der neuen Systematik der Inoceramen. Beitrage zur Kenntnis der Inoceramen XIV. *Mitteilungen aus der Mineralogisch-Geologischen Staatsinstitut in Hamburg*, **13**: 1–28.

—— 1933. Inoceramen von Madagaskar und ihre Bedeutung für die Kreide-Stratigraphie. *Zeitschrift der Deutschen geologischen Gesellschaft*, **85**: 241–259, pls 16–22.

Jolkicev, N.A., 1961. Inoceramen aus dem Maastricht bulgariens. *Travaux sur la Géologie de Bulgarie, Sofia; serie Paleontologie*, **4**: 133–69, pls 1–8 [In Bulgarian, with Russian and German summaries].

Kner, R. 1850. Versteinerungen des Kreidemergels von Lemberg und seiner Umgebung. *Naturwissenschaftliche Abhandlungen, Wien*, **3** (2): 42 pp., 5 pls.

Mercy, N. de 1877. Description de l'*Inoceramus Mantelli. Memoires de la Societe linnéenne de Nord de France, Amiens*, **4**: 324–34, pls 1, 2.

Nolan, S.C., Skelton, P.W., Clissold, B.P. & Smewing, J.D. 1990. Maastrichtian to early Tertiary stratigraphy and palaeogeography of the Central and Northern Oman Mountains. *In* **Robertson A.H.F., Searle, M.P. & Ries, A.C.** (editors), The Geology and Tectonics of the Oman Region. *Geological Society of London, Special Publication*, **49**: 495–519.

Orbigny A. d' 1844. *Paleontologie française; Terrains crétacées*, vol. 3, *Mollusques*: 807 pp., pls 237–489. G. Masson, Paris.

Reyment, R. A. 1958. Upper Cretaceous Mollusca (lamelliBranchia and Gastropoda) from Nigeria. *Colonial Geology and mineral resources*, **5** (2): 127–55, 4 pls.

Seitz, O. 1961. Die Inoceramen des Santon von Nordwestdeutchland. 1. Teil (Die Untergattungen *Platyceramus, Cladoceramus* und *Cordiceramus*). *Beihefte zum Geologischen Jahrbuch*, **46**: 3–186, pls 1–15.

—— 1967. Die Inoceramen des Santon und Unter-Campan von Nordwestdeutschland III, Teil, Taxonomie und Stratigraphie der Untergattungen, *Endocostea, Platyceramus, Cladoceramus, Selenoceramus* und *Cordiceramus* mit besonderer Berucksichtigung des Parasitismus bei diesen Untergattungen. *Beihefte zum Geologischen Jahrbuch*, **75**: 1–171, pls 1–27.

Sornay, J. 1957. *Palaeontologia Universalis*, no. 57, 2pp.

—— 1962. Etude d'une faune d'Inocerames du Senonien supérieur des

Charentes et description d'une espece nouvelle du Senonien de Madagascar. *Bulletin de la Société géologique de France*, (7) **4**: 118–122.

—— 1973. Sur les inocerames du Maestrichtien de Madagascar et une espece de la Craie à Baculites du NW de la France. *Annales de Paleontologie (Invertebres)*, **59** (1): 80–93, pls 1–4.

—— 1976. La faune d'inocerames de Dau (Region de Royan, Charente-Maritime) et remarques sur deux especes de d'Orbigny: *I. regularis* et *I. goldfussi*. *Annales de Paleontologie (Invertebres)*, **62:** 1–12, 5 figs, 5 pls.

Tzankov, T., Pamouktchiev, A., Tchechmedjieva, V. & Motekova, N. 1981. *Les Fossiles de Bulgarie, V. Cretace Superieur, Grandes Foraminiferes, Anthozoaires, Gasteropodes, Bivalvia*. 233 pp., 98 pls. *Editions de L'Academie Bulgare des Sciences, Sofia*.

Whitfield, R.P. 1877. *Preliminary Report on the Paleontology of the Black Hills, containing descriptions of new species of fossils from the Potsdam, Jurassic, and Cretaceous formations of the Black Hills of Dakota. United States Geographical and Geological Survey of the Rocky Mountain Region*. 49 pp. Washington, Government Printing Office.

—— 1880. Paleontology of the Black Hills of Dakota. Section iv. Fossils from the Cretaceous Rocks. Pp. 329–347 *In* Newton, H. & Jenney, W.P., 1880, Report on the geology and resources of the Black Hills of Dakota. *United States Geographical and Geological Survey, Rocky Mountains Region*. Washington.

—— 1885. Brachiopoda and LamelliBranchiata of the Raritan Clays and Greensand Marls of New Jersey. *Monographs of the United States Geological Survey*, **9**: 269 pp., 35 pls.

Zittel, K.A. 1865–66. Die Bivalven der Gosaugebilde. *Denkschriften der Kaiserlichen Akademie der Wissenschaften, Wien; Mathematisch-Naturwissenschaften Klasse*, **24** (2) (1865): 105–177, pls 1–10; **25** (2) (1866): 77–198, pls 11–27.

Bull. nat. Hist. Mus. Lond. (Geol.) **51**(2):267–273 Issued 30 November 1995

Late Campanian-Maastrichtian Bryozoa from the United Arab Emirates-Oman border region

PAUL D. TAYLOR

Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD

SYNOPSIS. Seven species of bryozoans have been found encrusting cobbles from the Qahlah Formation (Upper Campanian or Maastrichtian) of Jebel Huwayyah, east of Al Ain, UAE. This preliminary report describes and figures the Jebel Huwayyah bryozoan fauna and draws attention to its importance as a rare example of a bryozoan fauna from the Cretaceous tropics. The following taxa are described: *Bullaconopeum nodosum* gen. et sp. nov., *Biaviculigera* sp., *Pelmatopora* sp., *Leptocheilopora* sp., *Tecatia* sp., *Voigtopora* sp. and '*Berenicea*' sp.

INTRODUCTION

Bryozoans are sessile, suspension-feeding, colonial invertebrates, predominantly marine and typically with fossilizable skeletons of calcite. They often form a major component of Upper Cretaceous marine biotas: in north-west Europe individual assemblages sometimes contain a hundred or more species (e.g. Voigt 1973; Taylor 1987). Cretaceous bryozoans from other parts of the world are much less well-known and appear to be relatively low in both diversity and abundance. Nevertheless, Upper Cretaceous faunas have been found in regions as far apart as North America, India and Western Australia. However, bryozoans of this age have yet to be described from the Arabian Peninsula.

This paper is a preliminary description of a well-preserved fauna of encrusting bryozoans from the Qahlah Formation (Nolan *et al.* 1990; Skelton *et al.* 1990) of the Oman Mountains. The Qahlah Formation is late Campanian or early Maastrichtian in age (A. B. Smith *et al*, this volume). In the Jebel Huwayyah area it is thought to represent a transgressive fan delta depositional system (Skelton *et al.* 1990). The bryozoans were collected from Bed 7 of A. B. Smith *et al.* (this volume, Fig. 8) where they encrust cobbles together with the oyster *Acutostrea* and colonial corals. Although Smith *et al.* interpreted this bed as a shoreface facies, the moderately high diversity and general composition of the bryozoan fauna (with only one malacostegan) suggests a subtidal origin.

The seven bryozoan taxa found in the Qahlah Formation extend the geographical ranges of some genera formerly unrecorded in the Middle East. The bryozoans have particular significance in providing a rare glimpse of a tropical Cretaceous bryozoan fauna which can be compared with the temperate to subtropical faunas found elsewhere, notably in north-west Europe. Six of the seven species are identified to genus level only, pending further study and availability of additional material. The seventh species is distinctive and is represented by sufficient material to warrant its description as a new genus and species.

SYSTEMATIC PALAEONTOLOGY

All of the material is from the Qahlah Formation (Upper Campanian or Maastrichtian), Bed 7, SE corner of Jebel Huwayyah 1 (see A. B. Smith *et al.*, this volume), east of Al Ain, UAE/Oman borders (Sheet NG–40–14D; 1:100,000 grid reference CM 842878). Specimens are registered in the collections of The Natural History Museum, London. Scanning electron micrographs were prepared from uncoated specimens, imaged using back-scattered electrons (see Taylor 1986).

Cheilostome classification used here follows Gordon (1989), although it is recognized that analysis of phylogenetic relationships must precede a more satisfactory scheme.

Order **CHEILOSTOMIDA** Busk, 1852
Suborder **MALACOSTEGINA** Levinsen, 1902
Superfamily **MEMBRANIPOROIDEA** Busk, 1854
Family **ELECTRIDAE** Stach, 1937
Genus ***BULLACONOPEUM*** nov.

TYPE SPECIES. *Bullaconopeum nodosum* sp. nov.; Upper Cretaceous, Qahlah Formation, Oman Mountains.

NAME. Combination of *bulla* (Latin, knob, in reference to the tubercles) with the established bryozoan genus *Conopeum* (Latin, mosquito net).

DIAGNOSIS. Colony encrusting, multiserial; autozooidal opesia ovoidal, distal part smooth and crescent-shaped; cryptocyst pustulose, broad proximally, moderately broad laterally but absent distally; gymnocyst narrow, occasionally more extensive proximally; four gymnocystal tubercles present, two located near proximo-lateral corners of cryptocyst, two at distal edges of cryptocyst where crescent-shaped distal part of opesia begins; kenozooids occasionally developed, irregular in shape, with pustulose cryptocyst surrounding entire opesia, lacking the crescent-shaped smooth distal area of autozooids; pore chambers apparently lacking; intramural buds present, closure plates not observed; ovicells and avicularia not seen, presumed absent; early astogeny unknown.

REMARKS. This new monospecific genus is distinguished by the presence of four blunt tubercles around the edges of the autozooidal cryptocyst. The crescentic shape of the distalmost part of the opesia arching between the two disto-lateral tubercles is also characteristic and is presumably more-or-less coincident with the location of the orifice and operculum in the living zooid. The absence of ovicells supports assignment of *Bullaconopeum* to the malacostegans, a paraphyletic grade of primitive cheilostomes which at the present day have non-brooded planktotrophic larvae (cyphonautes). This is corroborated by the fact that avicularia are also lacking, even in areas of zooidal crowding where they might be expected to be found but where kenozooids are developed instead. Among malacostegan genera, *Bullaconopeum* resembles *Eokotosokum* Taylor & Cuffey, 1992, from the Maastrichtian of Alberta. This Canadian genus shows a similar development of the cryptocyst but has two large disto-lateral spine bases and no tubercles. Several other malacostegan genera (e.g. *Charixa*, *Spinicharixa*, *Villacharixa*; see Taylor & Cuffey 1992) possess spine bases which are lacking in *Bullaconopeum*, although it is possible that the tubercles of *Bullaconopeum* represent an evolutionary development from articulated spines. Tubercles occur in some malacostegan and other cheilostome genera. Voigt (1992) observed that they were especially common in bryozoans living in high energy environments (e.g. on algal fronds), were often variably present, and suggested that they may function in preventing mechanical damage. In contrast, the tubercles of *Bullaconopeum* are always present and occur in colonies living in protected microhabitats such as burrows.

Two families of malacostegans are recognized: Electridae and Membraniporidae. *Bullaconopeum* is provisionally assigned to the former family, which is much more diverse, but confident placement must await the discovery of early astogenetic stages to ascertain whether the ancestrula is simple (Electridae) or twinned (Membraniporidae).

Bullaconopeum nodosum sp. nov. Pl. 1

HOLOTYPE. BMNH BZ 3167.

PARATYPES. BMHN BZ 3168 (1), 3172 (1), 3173.

NAME. From *nodus* (Latin, knot), in reference to the node-like tubercles.

DESCRIPTION. Colonies are encrusting and sheet-like (Pl. 1, fig. 1), attaining a maximum diameter of at least 25 mm. None of the available specimens show unequivocal early astogenetic stages and therefore nothing is known of the ancestrula or early budding pattern. Abraded parts of colonies (Pl. 1, fig. 6) show that the basal wall of the zooids are fully calcified but that pore chambers are lacking.

Autozooids have a rounded rhomboidal shape and are relatively broad (Pl. 1, figs 2–3). In the holotype frontal length of the autozooids averages 0·38 mm (range = 0·32–0·47 mm; n = 15) and frontal width 0·35 mm (range = 0·27–0·39 mm; n = 15). An elongate ovoidal opesia occupies much of the frontal area of the autozooid. Opesial length in the holotype averages 0·27 m (range = 0·24–0·30 mm; n = 15) and opesial width 0·19 mm (range = 0·17–0·21 mm; n = 15). Cryptocyst borders the opesia proximally and laterally, whereas gymnocyst, slightly raised to form a distinctive semi-circular crescent, defines the distalmost edge of the opesia. The cryptocyst is pustulose, and is widest and shelf-like proximally but narrows and slopes more steeply inwards along the lateral edges of the opesia. The perimeter of the cryptocyst is slightly depressed relative to the surrounding gymnocyst, and the cryptocyst:gymnocyst boundary is well-defined and minutely beaded. The smoothly calcified gymnocyst forming the outer edge of the autozooid is narrow, especially laterally. Four conspicuous but short tubercles occur along the inner edge of the gymnocyst. Tubercle diameter is about 40–50 μm. The proximo-lateral pair of tubercles are located approximately level with, or a little proximally of, the proximal edge of the opesia. They mark the transition from the proximal gymnocyst to the narrower lateral gymnocyst. The disto-lateral pair of tubercles are situated where the pustulose cryptocyst ends and is replaced by gymnocyst forming the characteristic crescent-shaped distal edge of the opesia. Closure plates have not been observed, although some zooids are plugged with sediment which bears a superficial resemblance to a closure plate. Intramural buds are developed in some autozooids as an additional rim of cryptocyst within the opesia (Pl. 1, fig. 5).

Kenozooids are present sporadically (Pl. 1, fig. 4). They are slightly smaller than the autozooids and more irregularly shaped. Tubercles are lacking, the opesia is reduced relative to that of an autozooid, and cryptocyst surrounds the entire opesia, unlike autozooids where it is absent distally.

Ovicells and avicularia have not been found and are presumed to be absent.

REMARKS. *Bullaconopeum nodosum* is the most conspicuous and commonest of the bryozoans encrusting the collection of cobbles from Jebel Huwayyah. Colonies occur within pre-cementation burrows as well as on cobble surfaces where they are less well-preserved. Colony-form and zooid dimensions resemble those found in *Biaviculigera* sp. This similarity is readily appreciated as superficial when the two species are studied using SEM (compare Pl. 1, fig. 2 with Pl. 2, fig. 1).

Suborder **NEOCHEILOSTOMINA** d'Hondt, 1985
Infraorder **PSEUDOMALACOSTEGOMORPHA** d'Hondt, 1977
Family **CALLOPORIDAE** Norman, 1903
Genus ***BIAVICULIGERA*** Voigt, 1989

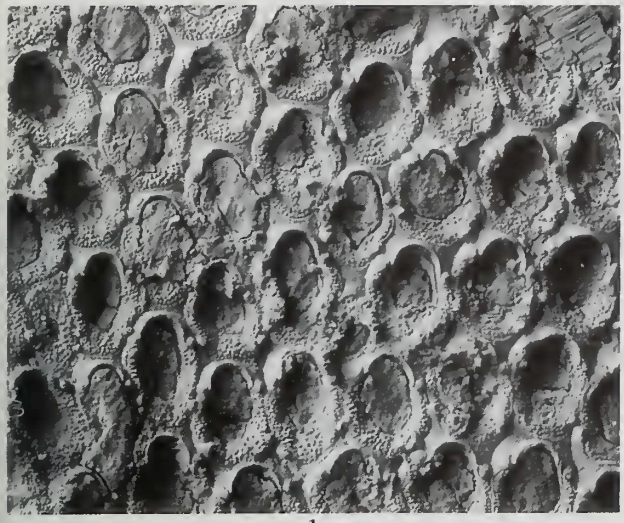
Biaviculigera sp. Pl. 2, fig. 1

MATERIAL. BZ 3171.

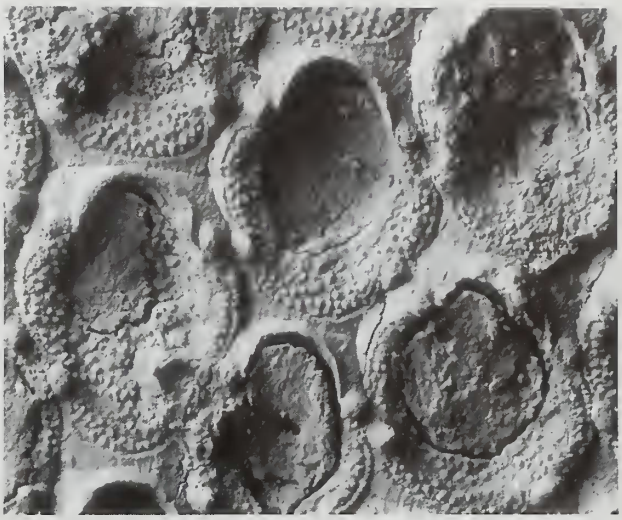
REMARKS. A well-preserved specimen of an unidentified

PLATE 1

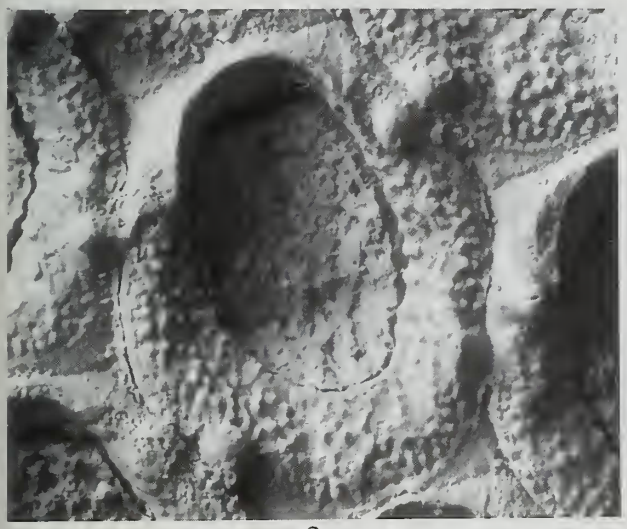
Figs 1–6 *Bullaconopeum nodosum* gen. et sp. nov., Qahlah Formation (Upper Campanian or Maastrichtian), Bed 7 of Smith *et al.* (this volume), SE corner of Jebel Huwayyah 1, east of Al Ain, UAE/Oman borders. **1–4**, BMNH BZ 3167, **holotype**; **1**, multiserial arrangement of zooids, × 35; **2**, group of autozooids showing tubercles and pustulose cryptocysts, × 90; **3**, autozooid with sediment-filled opesiae, × 150; **4**, kenozooid partly filled by sediment, × 120. **5–6**, BMNH BZ 3168 (1); **5**, autozooid (? astogenetically early) at preserved lateral edge of colony showing proximo-lateral pore window (right of centre) and intramural bud, × 150; **6**, abraded growing edge exposing calcified basal walls of zooids and vertical walls seemingly lacking pore chambers, × 90.



1

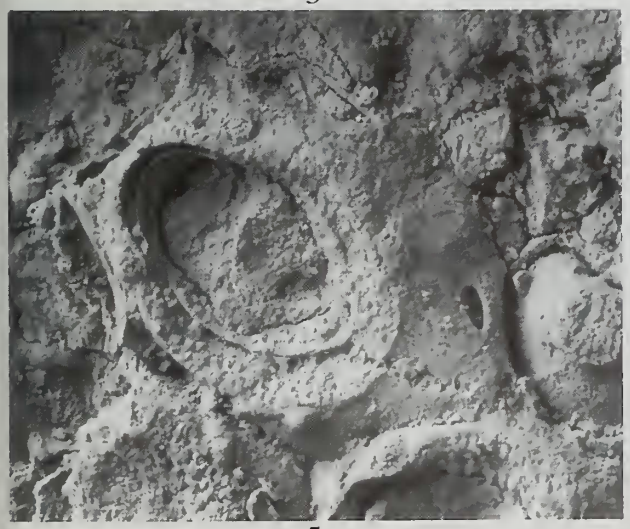


2



3

4



5

6

species of *Biaviculigera* has a sheet-like encrusting colony with spineless autozooids, non-pustulose cryptocysts, avicularia and ovicells. This genus (type species *Membranipora praecipua* Brydone, 1914) was proposed by Voigt (1989) for nine species of Cenomanian-Maastrichtian cheilostomes, seven of which were formerly assigned to the genus *Membranipora* as used in its broadest sense. *Biaviculigera* is characterized by having two types of avicularia. In the Qahlah Formation species these comprise large avicularia with spatulate rostra and small avicularia with pointed rostra.

Suborder **ASCHOPHORINA** Levinsen, 1909
Infraorder **CRIBRIOMORPHA** Lang, 1916
Family **PELMATOPORIDAE** Lang, 1916
Genus ***PELMATOPORA*** Lang, 1916

Pelmatopora sp. Pl. 2, fig. 2

MATERIAL. BZ 3170.

REMARKS. *Pelmatopora* is a diverse genus which ranges from the Coniacian to the Upper Campanian or possibly Danian (Larwood 1962). The Qahlah Formation species has about 16–20 arched costae, each with a large pelma (pore) in the narrow median area of costal fusion. Pelmatidia and lateral costal fusions seem to be absent, and 'interzooecial secondary tissue' (sensu Larwood 1962) and oral spines have not been observed. However, sediment obscures much of the morphological detail. A few zooids bear ovicells, and many have small paired avicularia located on either side of the high autozooidal orifice, inwardly directed towards the orifice, spatulate and with well-developed transverse bars.

Genus ***LEPTOCHEILOPORA*** Lang, 1916

Leptocheilopora sp. Pl. 2, fig. 3

MATERIAL. BZ 3169 (3).

REMARKS. An inconspicuous colony of *Leptocheilopora* encrusts one of the cobbles. The small autozooids have about 14–16 closely-spaced costae forming a flat frontal shield. Four oral spines are present and there are numerous small avicularia, each with a relatively large proximal gymnocyst and a spatulate rostrum without a transverse bar. Lateral costal fusions and pelmata have not been observed. The orifice has well marked lateral constrictions, dividing a deep poster from the distal anter. None of the species of *Leptocheilopora* revised by Larwood (1962) compares closely with the Qahlah Formation species, especially with regard to the avicularia which are uncommon in this genus. In Europe *Leptocheilopora* ranges from the Santonian to the Maastrichtian (Larwood 1962).

Infraorder **HIPPOTHOOMORPHA** Gordon, 1989
Family **HIPPOTHOIDAE** Fischer, 1866
Genus ***TECATIA*** Morris, 1980

Tecatia sp. Pl. 2, fig. 4

MATERIAL. BZ 3168 (2).

REMARKS. The tiny autozooids of this ascophoran are dispersed widely across the substratum, and arranged in a seemingly chaotic manner. It is unclear whether the wide-spacing of the autozooids is because they have long caudae, are interspersed with stolon-like heterozooids, or reflects loss of intervening zooids. The autozooidal orifice has a distinct sinus, and the strongly arched gymnocystal frontal wall shows a line of pore windows just above substratum level. Although this species is assigned to *Tecatia*, the minute pores in the frontal wall which are characteristic of *Tecatia* have not been observed, possibly because of preservational limitations.

Tecatia is represented by four species from the Upper Maastrichtian of the type area and one Recent species from the Pacific coast of North and Central America (Morris 1980; Voigt & Hillmer 1983). Voigt (1987) described how *T. minuta* Morris, 1980, can be found in 'minicaverns' formed by thalassinoid burrows in hardgrounds in the Maastrichtian Chalk Tuff. Similarly, the Qahlah Formation species of *Tecatia* inhabited the cryptic habitats provided by precementational burrow systems in cobbles.

Order **CYCLOSTOMATA** Busk, 1852
Suborder **TUBULIPORINA** Milne Edwards, 1838
Family **STOMATOPORIDAE** Pergens & Meunier, 1886
Genus ***VOIGTOPORA*** Bassler, 1952

Voigtopora sp. Pl. 2, fig. 5

MATERIAL. BZ 3169 (1), 3172 (2).

REMARKS. A few colonies of the runner-like cyclostome *Voigtopora* encrust the cobbles. This genus is distinguished from the related *Stomatopora* by the presence of lateral branch ramifications and the long proximal extensions of the zooids which flank the previous zooid in linear series (see Illies 1976). *Voigtopora* appears to range from the Hauterivian to the Campanian in Europe (Pitt & Taylor 1990), and also occurs in the Albian and Cenomanian of Texas. The species-level systematics of this genus is in need of revision, with characters of early colony development likely to be of considerable importance.

PLATE 2

Figs 1–6 Bryozoans from the Qahlah Formation (Upper Campanian or Maastrichtian), Bed 7 of Smith *et al.* (this volume), SE corner of Jebel Huwayyah 1, east of Al Ain, UAE/Oman borders; **1**, *Biaviculigera* sp., BMNH BZ 3171, part of colony showing autozooids with smooth cryptocysts, a large spatulate avicularium (in recess, centre left), and several small acuminate avicularia, × 60; **2**, *Pelmatopora* sp., BMNH BZ 3170, autozooid (partly obscured by sediment) showing large pelmata in median area of costal fusion, × 100; **3**, *Leptocheilopora* sp., BMNH BZ 3169 (3), autozooid flanked by two small, abraded avicularia, × 230; **4**, *Tecatia* sp., BMNH BZ 3168 (2), oblique view of a zooid with sediment-plugged orifice (arrow) and line of basal pore windows, × 250; **5**, *Voigtopora* sp., BMNH BZ 3169 (1), branch with three zooids viewed obliquely, × 45; **6**, '*Berenicea*' sp., BMNH BZ 3169 (2), part of colony showing transversely-wrinkled frontal walls, × 45.

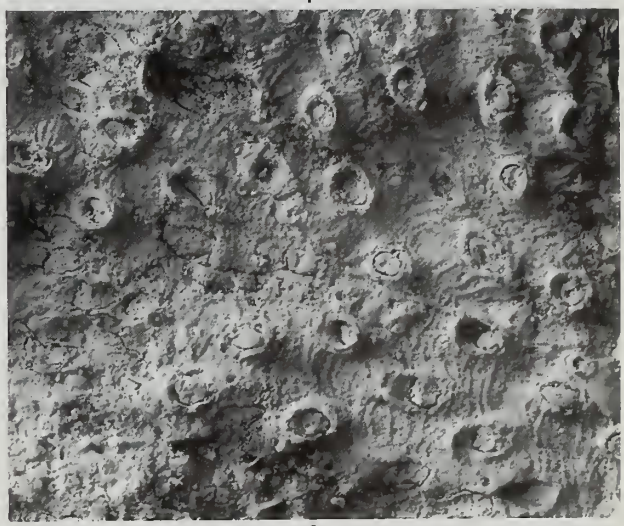
1

2

3

4

5



6

Family incertae sedis
Genus *'BERENICEA'* Lamouroux, 1821

'Berenicea' sp. Pl. 2, fig. 6

MATERIAL. BZ 3169 (2).

REMARKS. Part of a sheet-like tubuliporine cyclostome is present at the edge of one of the burrows. The zooidal frontal walls are transversely wrinkled, but in the absence of gonozooids it is impossible to assign the colony to a genus. Therefore, following the procedure adopted by Taylor & Sequieros (1982) and Pitt & Taylor (1990), the specimen is placed in the informal genus '*Berenicea*'.

DISCUSSION

This new bryozoan fauna has both palaeobiogeographical and palaeoecological importance. As noted above, the great majority of Cretaceous bryozoan faunas have been described from Europe. Nothing was previously known of Upper Cretaceous bryozoan faunas from the Arabian Peninsula. The Qahlah Formation specimens therefore fill a major geographical gap in our knowledge of Upper Cretaceous bryozoans. Furthermore, as the late Cretaceous proto-Oman Mountains would have been located almost on the palaeoequator (e.g. A. G. Smith *et al.* 1994), it provides a tropical fauna that can be compared with the temperate faunas of Europe and elsewhere. Six of the seven genera found in the Qahlah Formation occur also in north-west Europe, the exception being *Bullaconopeum*. At the genus-level, therefore, it is seems that there was little taxonomic differentiation between late Cretaceous temperate and tropical bryofaunas. In addition, albeit based on a small number of species, the proportion of cheilostomes (five species) to cyclostomes (two species) in the tropical Qahlah Formation is fairly typical for a fauna of this age (cf. Lidgard *et al.* 1993, fig. 7).

Along with other cemented invertebrates and plants, bryozoans are commonly found encrusting the surfaces of cobbles like those from the Qahlah Formation. Cobbles provide a variety of different microhabitats for these sessile organisms, including upper and lower external surfaces, and crevices formed by vacated borings or pre-cementational burrows. Therefore, cobbles allow the study of small scale niche differentiation among demonstrably in-situ organisms. Few studies of cobble-dwellers have been undertaken in the fossil record, and the only detailed study involving a diverse Cretaceous bryozoan fauna is that of Wilson (1986) on cobbles from the Aptian Faringdon Sponge Gravel of England. Wilson found a clear distinction between species colonizing the outer surfaces of the cobbles, which were robust in morphology, and species living in vacated borings, which often had a delicate construction. This he interpreted as a consequence of the physical rigours experienced by the encrusters on outer surfaces compared with the protected burrows. Preliminary study suggests that a similar differentiation may occur among the colonizers of the Qahlah Formation cobbles, although further field sampling and careful mapping of distributions will be needed to substantiate this impression. It would be particularly instructive to compare the cyclostome-dominated Aptian Faringdon Sponge Gravel cobbles with the cheilostome-dominated younger Qahlah Formation cobbles.

ACKNOWLEDGEMENTS. For discussion and advice on matters bryozoological and stratigraphical, I wish to thank Ehrhard Voigt, Peter Skelton, Noel Morris, Andrew Smith and Andrew Gale.

REFERENCES

Bassler, R. S. 1952. Taxonomic notes on some genera of fossil and Recent Bryozoa. *Journal of the Washington Academy of Science*, **42**: 381–385.

Brydone, R. M. 1914. Notes on new or imperfectly known Chalk Polyzoa. *Geological Magazine*, (decade 6), **1**: 481–483.

Busk, G. 1852. An account of the Polyzoa, and sertularian Zoophytes, collected in the Voyage of the Rattlesnake, on the Coasts of Australia and the Loisiade Archipelago, &c. *In*: MacGillivray, J., *Narrative of the Voyage of H.M.S. Rattlesnake, during the years 1846–1850, vol. 1*: 343–402. London.

—— 1854. *Catalogue of marine Polyzoa in the collection of the British Museum, II. Cheilostomata (part)*, pp. 55–120. London.

Fischer, P. 1866. Étude sur les bryozoaires perforants de la Famille des Térébriporides. *Nouvelles Archives du Muséum d'Histoire Naturelle de Paris*, **2**: 293–313.

Gordon, D. P. 1989. The marine fauna of New Zealand: Bryozoa: Gymnolaemata (Cheilostomida Ascophorina) from the western South Island continental shelf and slope. *New Zealand Oceanographic Institute Memoir*, **97**: 1–158.

d'Hondt, J.-L. 1977. Valeur systématique de la structure larvaire et des particularités de la morphogenèse post-larvaire chez les bryozoaires gymnolaemates. *Gegenbaurs Morphologisches Jahrbuch*, **123**: 463–483.

—— 1985. Contribution à la systématique des Bryozoaires Eurystomes. Apports récents et nouvelles propositions. *Annales des Sciences Naturelles, Zoologie*, (13), **7**: 1–12.

Illies, G. 1976. Budding and branching patterns in the genera *Stomatopora* BRONN, 1825 and *Voigtopora* BASSLER, 1952. *Oberrheinische Geologische Abhandlungen*, **25**: 97–110.

Lamouroux, J. 1821. *Exposition méthodique des genres de l'ordre des polypiers*. viii + 115 pp. Paris.

Lang, W. D. 1916. A revision of the 'cribrimorph' Cretaceous Polyzoa. *Annals and Magazine of Natural History*, (8), **18**: 81–112, 381–410.

Larwood, G. P. 1962. The morphology and systematics of some Cretaceous Cribrimorph Polyzoa (Pelmatoporinae). *Bulletin of the British Museum (Natural History), Geology Series*, **6**: 1–285, pls 1–23.

Levinsen, G. M. R. 1902. Studies on Bryozoa. *Videnskabelige Meddeleser fra den naturhistoriske Forening i København*, **54**: 1–31.

—— 1909. *Morphological and systematic studies on the cheilostomatous Bryozoa*. 431 pp. Copenhagen.

Lidgard, S., McKinney, F. K. & Taylor, P. D. 1993. Competition, clade replacement, and a history of cyclostome and cheilostome bryozoan diversity. *Paleobiology*, **19**: 352–371.

Milne Edwards, H. 1838. Mémoire sur les Crisies, les Hornères et plusieurs autres polypes vivants ou fossiles dont l'organisation est analogue à celle des Tubulipores. *Annales des Sciences Naturelles, Zoology*, (2), **9**: 193–238.

Morris, P. A. 1980. The bryozoan family Hippothoidae (Cheilostomata Ascophora), with emphasis on the genus *Hippothoa*. *Monograph Series of the Allan Hancock Foundation*, **10**: 1–115.

Nolan, S. C., Skelton, P. W., Clissold, B. P. & Smewing, J. D. 1990. Maastrichtian to early Tertiary stratigraphy and palaeogeography of the Central and Northern Oman Mountains. *In*: Robertson, A. H. F., Searle, M. P. & Ries, A. C. (eds), The Geology and Tectonics of the Oman Region. *Geological Society Special Publication*, **49**: 495–519.

Norman A. M. 1903. Notes on the natural history of East Finmark. Polyzoa. *Annals and Magazine of Natural History*, (7), **11**: 567–598.

Pergens, E. & Meunier, A. 1886. La Faune des Bryozoires garumniens de Faxe. *Annales de la Société Rorale Malacologique de Belgique* **21**: 187–242.

Pitt, L. J. & Taylor, P. D. 1990. Cretaceous Bryozoa from the Faringdon Sponge Gravel (Aptian) of Oxfordshire. *Bulletin of the British Museum (Natural History), Geology Series*, **46**: 61–152.

Skelton, P. W., Nolan, S. C. & Scott, R. W. 1990. The Maastrichtian transgression onto the northwestern flank of the Proto-Oman Mountains: sequences of rudist-bearing beach to open shelf facies. *In* : Robertson, A. H. F., Searle, M. P. & Ries, A. C. (eds), The Geology and Tectonics of the Oman Region. *Geological Society Special Publication*, **49**: 521–547.

Smith, A. B., Morris, N. J. & Gale, A. S. In press [this volume]. Late

Cretaceous carbonate platform faunas from the United Arab Emirates and Oman borders region.

Smith, A. G., Smith, D. G. & Funnell, B. M. 1994. *Atlas of Mesozoic and Cenozoic coastlines*. 99 pp. Cambridge.

Stach, L. W. 1937. Lady Julia Percy Island. Reports of the McCoy Society for Field Investigation and Research. 13. Bryozoa. *Proceedings of the Royal Society of Victoria*, (n.s.), **49** (2): 374–384.

Taylor, P. D. 1986. Scanning electron microscopy of uncoated fossils. *Palaeontology*, **29**: 685–690.

—— 1987. Bryozoans. *In*: Smith, A.B. (ed.), *Fossils of the Chalk*, pp. 30–49. Palaeontological Association Field Guides to Fossils No. 2. London.

—— **& Cuffey, R. J.** 1992. Cheilostome bryozoans from the Upper Cretaceous of the Drumheller area, Alberta, Canada. *Bulletin of the British Museum (Natural History), Geology Series*, **48**: 13–24.

—— **& Sequeiros, L.** 1982. Toarcian bryozoans from Belchite in north-east Spain. *Bulletin of the British Museum (Natural History), Geology Series*, **37**: 117–129.

Voigt, E. 1973. Environmental conditions of bryozoan ecology of the hardground biotope of the Maastrichtian Tuff-Chalk, near Maastricht. *In*: Larwood, G. P. (ed.), *Living and fossil Bryozoa*. 185–197. London.

—— 1987. Thalassinoid burrows in the Maastrichtian Chalk Tuff near Maastricht (The Netherlands) as a fossil hardground microcavern biotope of Cretaceous bryozoans. *In*: Ross, J. R. P. (ed.), *Bryozoa: present and past*, pp. 293–300. Bellingham.

—— 1989. Beitrag zur Bryozoen-Fauna des sächsischen Cenomaniums. Revision von A. E. REUSS', 'Die Bryozoen des unteren Quaders' in H. B. GEINITZ' 'Das Elbthalgebirge in Sachsen' (1872). Teil I: Cheilostomata. *Abhandlungen des Staatlichen Museums für Mineralogie und Geologie zu Dresden*, **36**: 8–87, 170–183, 189–208 (pls 1–20).

—— 1992. Über die wahrscheinliche Funktion der Frontalwand-Tuberkeln als Distanzhalter bei cheilostomen Bryozoen (fossil und rezent). *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg*, (NF), **33**: 131–154.

—— **& Hillmer, G.** 1983. Oberkretazische Hippothoidae (Bryozoa Cheilostomata) aus dem Campanium von Schweden und dem Maastrichtium der Niederlande. *Mitteilungen aus dem Geologisch–Paläontologischen Institut der Universität Hamburg*, **54**: 169–208.

Wilson, M. A. 1986. Coelobites and spatial refuges in a Lower Cretaceous cobble-dwelling hardground fauna. *Palaeontology*, **29**: 691–703.

Bull. nat. Hist. Mus. Lond. (Geol.) **51**(2):275–276 Issued 30 November 1995

Maastrichtian brachiopods from the United Arab Emirates-Oman border region

ELLIS F. OWEN

Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD

INTRODUCTION

Brachiopods were particularly rare in the Maastrichtian sediments of the United Arab Emirates-Oman borders region. Despite intensive collecting only four specimens were found, all coming from the lower *Loftusia*-rich beds of the Qahlah Formation exposed at Jebel Huwayyah (see introduction for locality details). These four specimens belong to a hitherto undescribed genus of terebratulid.

SYSTEMATIC DESCRIPTIONS

Class **TEREBRATULIDA** Waagen, 1883
Suborder **TEREBRATULIDINA** Waagen, 1883
Superfamily **TEREBRATULACEA** Gray, 1840
Family **TEREBRATULIDAE** Gray, 1840
Genus ***PSEUDOGIBBITHYRIS*** nov.

TYPE SPECIES. *Pseudogibbithyris arabica* sp. nov.

DIAGNOSIS. Medium-sized uniplicate terebratulid, slightly longer than wide, elongate-oval in general outline and evenly biconvex. Umbo short, beak suberect, foraman small, permesothyrid. Cardinal process present, brachial loop simple.

REMARKS. *Pseudogibbithyris* differs from *Gibbithyris* and *Concinnithyris* from the European Upper Chalk (Senonian), which it resembles in external morphological features, in its distinctly flat bifid cardinal process, deep hinge-trough and short, triangular hinge-plates.

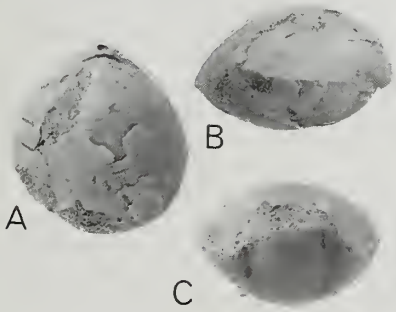


Fig. 1. *Pseudogibbithyris arabica* gen. et sp. nov., holotype, BMNH BF47; Jebel Huwayyah, section 2, beds 3–6. A, dorsal; B, lateral; C, anterior views: all × 1.

Pseudogibbithyris arabica sp. nov. Figs 1, 2

DIAGNOSIS. As for genus.

TYPES. Holotype, BMNH BF47; paratypes BMNH BF44–46.

DESCRIPTION. The dorsal valve is dominated by a low median fold bounded by faint carinae originating from a point midway between the umbonal area of the valve and the anterior margin of the shell. A corresponding shallow sulcus in the ventral valve forms a wide, shallow uniplication occupying the whole width of the anterior commissure.

Internal characters include a well-developed flat, but distinctly bifid cardinal process, and a deep hinge-trough. The hinge-plates are short, triangular in outline with a slightly concave ventral surface, and are deflected towards the dorsal valve. The triangular shape of the hinge-plates is maintained in the development of the horizontally placed bands of the descending branches of the brachial loop, which is uncomplicated and terminates in a very high arcuate transverse band.

REMARKS. The only morphological features which this species has in common with other Terebratulidae of the Upper Cretaceous are the distinctly oval general outline and uniplicate anterior commissure. The internal structure, notably the distinctive cardinalia and short triangular hinge-plates, are features more typical of terebratulid species of the Upper Jurassic to Lower Cretaceous, the closest comparison being to species of *Nucleata* and *Pygites*. However, it is not suggested that there is any direct relationship between the species described here as *Pseudogibbithyris arabica* gen. et sp. nov. and the Tithonian genera mentioned above. As no reference to any forms which could be confidently compared to this species are known, it is treated as a previously undescribed genus and species.

It would be unwise at this stage to draw any firm conclusions about the phylogenetic relations of this taxon. The simple cardinalia and brachial loop structure seen in the transverse serial sections (Fig. 2), is unusual and suggests a late Jurassic or early Cretaceous ancestry. However, the taxon should remain broadly assigned until more material is obtained, allowing further investigation.

OCCURRENCE. All specimens came from the *Loftusia*-rich facies (beds 3–6) Jebel Huwayyah, section 2 (see volume Introduction for locality details). They are Maastrichtian in age.

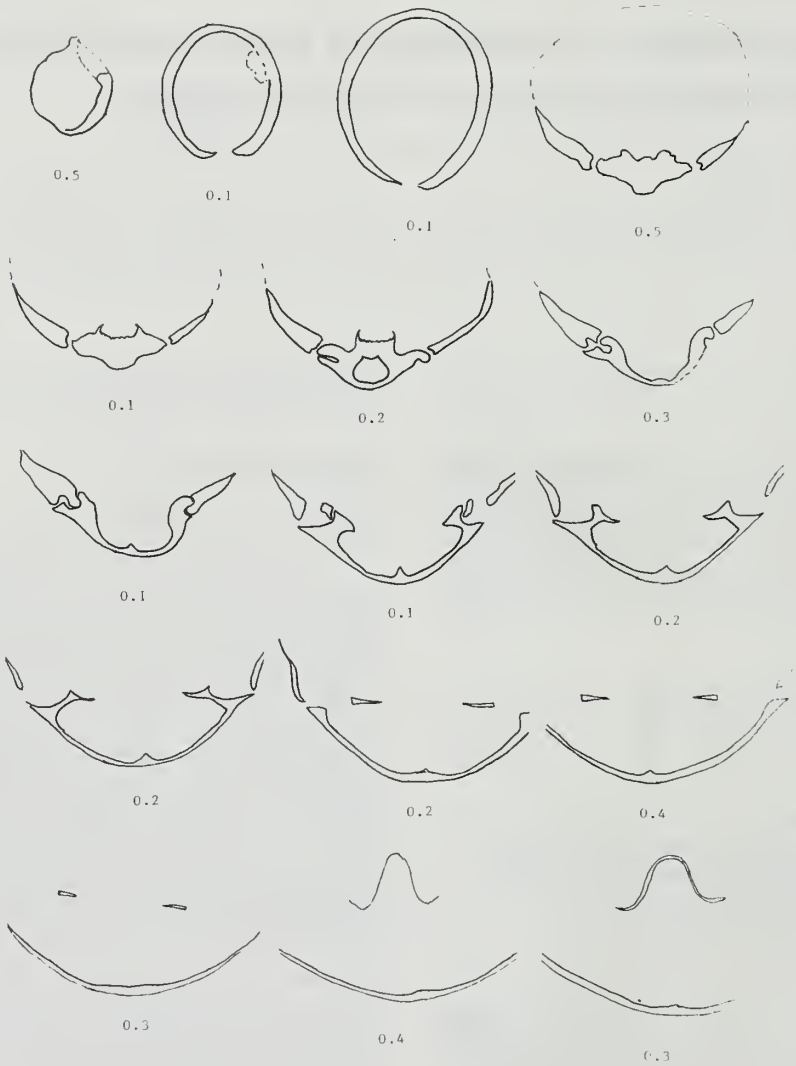


Fig. 2. Sixteen transverse serial sections through the holotype of *Pseudogibbithyris arabica* gen. et sp. nov. (BMNH BF47) from Jebel Huwayyah, section 2, beds 3–6. Note the bifid cardinal process (sections 5 & 6), the short triangular hinge-plates, and high, arcuate transverse band of the brachial loop. The numerals denote the distance in mm between each section. All × 3.

Bull. nat. Hist. Mus. Lond. (Geol.) **51**(2):277–305 Issued 30 November 1995

Late Campanian-Maastrichtian rudists from the United Arab Emirates-Oman border region

N. J. MORRIS

Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD

P.W. SKELTON

Department of Earth Sciences, The Open University, Walton Hall, Milton Keynes, Buckinghamshire MK7 6AA

CONTENTS

SYNOPSIS. About 30 species of Upper Campanian and Maastrichtian rudist bivalves from the Qahlah and Simsima Formations of the United Arab Emirates-Oman border region are described. They include *Semailia smithi* gen. et sp. nov. of the Dictyoptychidae, *Glabrobournonia arabica* gen. et sp. nov. of the Radiolitidae (Biradiolitinae), and *Pseudosabinia* gen nov. of the Radiolitidae (Joufiinae). The geological succession at Qarn Mulayh (Mileih), 7 km west of Jebel Buhays, is described.

STRATIGRAPHY AND AGE

In addition to the stratigraphy outlined by Smith, Morris and Gale at the beginning of this volume we include here stratigraphical details of the successions at Qarn Mulayh and Qarn Murrah (the 'red qarns') situated to the west of Jebels Buhays and Faiyah, UAE (Smith *et al.*, this volume, fig. 4). At these localities, limestone platform sedimentation on the serpentinized front of the Semail Ophiolite started earlier than in the jebels to the east, and is equivalent in age to the arenaceous facies of the Qahlah Formation.

A section at Qarn Mulayh is given in Fig. 1. Similar beds also form the majority of the outcrop at Qarn Murrah, to the north. On the basis of the rudists, we suspect that the succession at both qarns is of late Campanian age, and may possibly extend into the earliest Maastrichtian. These limestones correlate laterally with the sandy facies of the Qahlah Formation, with only a few of the species present above in the basal beds of the Simsima Formation.

Table 1 gives a full list of the rudists collected, and their distribution is shown in Fig. 2. The oldest fauna (1 on Fig. 2) occurs at Qarn Mulayh and Qarn Murrah, and also in the lower Qahlah Formation gravels at Jebels Huwayyah and Bu Milh. It is probably Campanian in age (the M1 fauna of Skelton *et al.*, 1990). The middle fauna (2 on Fig. 2) occurs in the upper Qahlah Formation *Loftusia*-Beds at Jebel Huwayyah, and the top Qahlah Formation gravels (with acteonellids) at Jebel Bu Milh. It is Campanian/early Maastrichtian in age (the intermediate M1/M2 fauna of Skelton *et al.*, 1990). The upper fauna (3 on Fig. 3) occurs in the main part of the Simsima Formation, at Jebels Faiyah, Buhays, Rawdah and Huwayyah. It is Maastrichtian in age.

The level 1 fauna compares closely with the so-called *Pironaea-Pseudopolyconites* Senonian fauna of Sladić-Trifunović (1989), for which the type area is the 'Vrbovać Beds' of eastern Serbia. Diagnostic novel taxa (not present in the older Gosau Beds) are: **Pironaea, Yvaniella, *Pseudopolyconites, Joufia, Neoradiolites, Branislavia (?=*Colveraia), Sabinia* [= **Pseudosabinia* here), and *Mitrocaprina* (asterisks denote those also in the UAR/Oman fauna). In addition, the following were noted by Sladić-Trifunović: **Vaccinites loftusi, V. ultimus, V. orientalis, V. bacevicensis, Hippurites colliciatus, ?*H. lapeirousei, *Hippuritella cornucopiae.* Moreover, Sladić-Trifunović (1989: 149) observed: 'The species **Vaccinites oppeli* Douvillé, also found in the Vrbovać Reef (Bačevića), is certainly of a special biostratigraphic importance, since it was previously believed to exist only in Early Senonian'.

Sladić-Trifunović (1989: 153), following the earlier works of Milovanović and Grubić, regarded the assemblage as Upper Campanian/Maastrichtian, mainly based on the supposed evolution of *Pironaea*. She did, however, acknowledge the arguments of others (for an earlier-extending range), based on orbitoids, and agreed that the fauna was probably absent from the Upper Maastrichtian. Pejović & Radoičić (1987) for example, had revised the age of the 'Brač Marbles' (with *Pironaea* etc) to the Lower-Middle Campanian. Sladić-Trifunović (1989: 154) responded: 'If the 'Brač Marbles', which include *P. milovanovici* [Kühn's species, regarded as

Table 1 Systematic list of the rudists found in the Qahlah and Simsima Formations.

Family CAPROTINIDAE Gray, 1848
Genus *GYROPLEURA* Douvillé, 1887
Gyropleura sp.

Family PLAGIOPTYCHIDAE MacGillavry, 1937
Genus *PLAGIOPTYCHUS* Matheron, 1843
Plagioptychus cf. *toucasianus* Matheron, 1843

Family DICTYOPTYCHIDAE Skelton *in* Skelton and Benton, 1993
Genus *DICTYOPTYCHUS* Douvillé, 1905
Dictyoptychus morgani (Douvillé, 1904)
Genus *EODICTYOPTYCHUS* Skelton & El-Asa'ad, 1992
Eodictyoptychus aff. *arumaensis* Skelton & El-Asa'ad, 1992
Genus *SEMAILIA* Morris & Skelton, gen. nov.
Semailia smithi Morris & Skelton sp. nov.
Semailia sp.

Family HIPPURITIDAE Gray, 1848
Subfamily TORREITINAE Grubić, 1979
Genus *Torreites* Palmer, 1933
Torreites sanchezi (Douvillé, 1927) *milovanovici* Grubić, 1980
Subfamily HIPPURITINAE Gray, 1848
Genus *VACCINITES* Fischer, 1887
Vaccinites loftusi (Woodward, 1855)
Vaccinites vesiculosus (Woodward, 1855)
Vaccinites oppeli (Douvillé, 1892)
Genus *HIPPURITES* Lamarck, 1801
Hippurites aff. *lapeirousei* Goldfuss, 1841
Hippurites cornucopiae Defrance, 1821
Hippurites aff. *cornucopiae* Defrance, 1821
Genus *PIRONAEA* Meneghini *in* Pirona, 1868
Pironaea cf. *polystyla* Pirona, 1868

Family RADIOLITIDAE d'Orbigny, 1847
Subfamily RADIOLITINAE d'Orbigny, 1847
Genus *Praeradiolites* Douvillé, 1902
Praeradiolites cf. *subtoucasi* Toucas, 1907
Genus *Radiolites* Lamarck, 1801
?*Radiolites* sp.
Subfamily PSEUDOPOLYCONITINAE Sladić-Trifunović, 1983
Genus *Pseudopolyconites* Milovanović, 1937
Pseudopolyconites aff. *parvus* Milovanović, 1935
Subfamily BIRADIOLITINAE Douvillé, 1902
Genus *Biradiolites* d'Orbigny, 1850
Biradiolites aff. *baylei* Toucas, 1909
?*Biradiolites* aff. *baylei* Toucas, 1909
Genus *Glabrobournonia* Morris & Skelton gen. nov.
Glabrobournonia arabica Morris & Skelton sp. nov.
Sub-family SAUVAGESIINAE Douvillé, 1908
Genus *Durania* Douvillé, 1908
Durania cf. *gaensis* (Dacqué, 1903)
Durania cf. *apula* (Parona, 1900)
Durania form A
Durania form B
Durania spp.
Subfamily LAPEIROUSIINAE Kühn, 1932
Genus *Lapeirousia* Bayle, 1878
Lapeirousia sp.
Genus *Osculigera* Kühn, 1932
Osculigera cf. *vautrinioides* Vogel, 1970
Subfamily JOUFIINAE Karacabey-Öztemür 1981
Genus *Colveraia* Klinghardt, 1921
Colveraia aff. *variabilis* Klinghardt, 1921
Genus *Pseudosabinia* Morris & Skelton gen. nov.
Pseudosabinia aff. *klinghardti* (Boehm, 1927)

'advanced'], were accepted as being of the Upper Campanian age, there would be no sense in talking about the evolution of the genus *Pironaea*'. The *Pironaea* story has, indeed, been shown to be incorrect by J. M. Pons & E. Vicens (unpublished), who suggested that the different forms reflect ontogeny, rather than phylogeny, while Swinburne (1990: 27) dated the Brač Marbles (= Pućisča Formation) as early-middle Campanian, based on Sr isotope correlations, in agreement with Pejović & Radoičić. Moreover, by the same means, she and others (Swinburne *et al.*, 1992) re-assigned some *Pironaea* beds in Bulgaria, which had previously been placed at various levels in the Maastrichtian, to the Campanian and lowest Maastrichtian. Thus the '*Pironaea-Pseudopolyconites* Senonian' fauna seems to have ranged from the early Campanian to the earliest Maastrichtian. Additionally, Philip & Platel (1987) assigned their *Torreites* beds in Dhofar to the Campanian, based on orbitoids, while in the Caribbean the range of *Torreites sanchezi* (in our level 1 fauna) is also restricted to the Campanian (Rojas, Iturralde-Vinent, & Skelton, *in press*).

In summary, a Campanian age for the level 1 fauna seems the most plausible (though on the rudist evidence alone, we still cannot yet exclude the earliest Maastrichtian). On the other hand, the level 3 fauna presents a marked contrast, having only *V. oppeli, H. cornucopiae, Colveraia* and *Pseudosabinia* in common with the classic *Pironaea-Pseudopolyconites* Senonian fauna. *H. cornucopiae*, though, is also well known from the Maastrichtian of Sicily and elsewhere. As noted in Skelton *et al.* (1990: 545), this younger fauna is also characterized by some distinctive Arabian/Iranian endemics (e.g. *Dictyoptychus*). The Level 3 fauna is independently dated by ammonites (Kennedy, this volume) as late Early to early Late Maastrichtian.

SYSTEMATIC PALAEONTOLOGY

Most of the described and figured rudists are in the collections of The Natural History Museum, and are cited with the prefix BM; many of them have the additional prefix LL, and unless otherwise stated the specimens are in the Morris, Gale & Smith Collection; most of the other material is in the Skelton collection, collected by Skelton and Nolan (Skelton *et al*, 1990). The morphotype nomenclature used, eg. 'elevator', 'clinger', 'recumbent', is according to the scheme of Gili & Skelton (1994), summarised by Skelton (1991) and Ross & Skelton (1993).

Family **CAPROTINIDAE** Gray, 1848.
(*emend.* Skelton, 1978; =Monopleuridae Munier-Chalmas, 1873)
Genus ***GYROPLEURA*** Douvillé, 1887

TYPE SPECIES. *Requienia cenomanensis* d'Orbigny, 1850.

REMARKS. There are no accessory cavities.

Gyropleura sp. Pl. 1, fig. 2

MATERIAL. Four small specimens from top bed 4 or basal bed 5, Simsima Formation Jebel Rawdah, section 1, ammonite and inoceramid horizon; two are attached to the upper valve of an '*Umbonium*', BM LL41767–69.

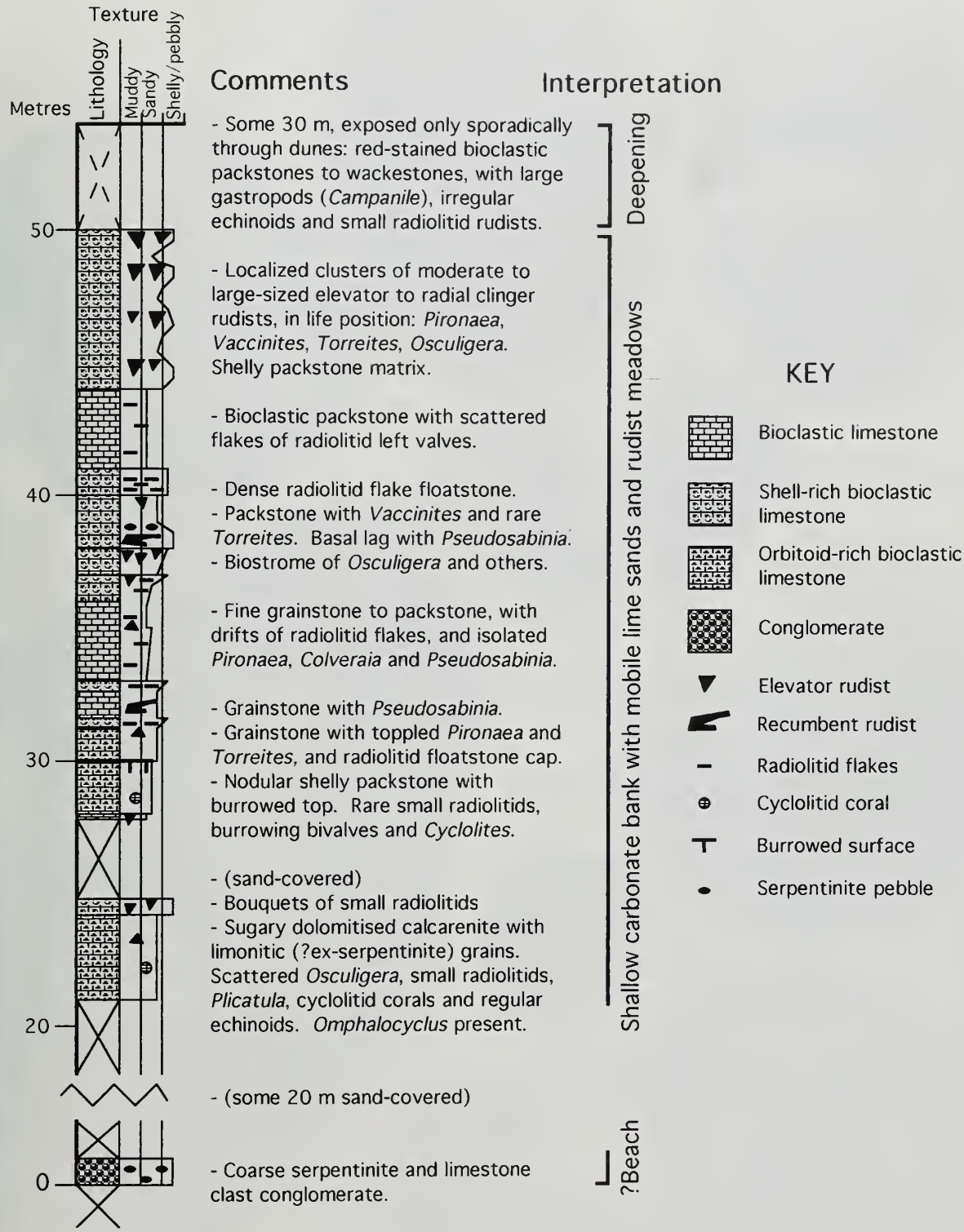


Fig. 1 Measured section at Qarn Mulayh (Mileih), 7 km west of Jebel Buhays; section logged at the north end of the western flank by P W Skelton.

Ut	Ps	Bi	Bo	Du	La	Os	Pk	Pr	Co	Eo	Se	Di	Pl	Pi	Vl	Vv	Vo	Hc	H	T
3		•	•	•	•		?	?	•		•	•	•				•	•	•	
2		•	•		•					•	•					•				
1	•		•	?		•	•	•	•	•				•	•	•				•

Fig. 2 Stratigraphical distribution of the rudists. Ut = stratigraphical units: 1 = lower part of the Qahlah Formation, 2 = upper part of the Qahlah Formation (the gravels and the *Loftusia*-Beds), 3 = Simsima Formation. Ps = *Pseudopolyconites*, Bi = *Biradiolites*, Bo = *Glabrobournonia*, Du = *Durania*, La = *Lapeirousia*, Os = *Osculigera*, Pk = *Pseudosabinia* aff. *klinghardti*, Pr = *P. 'rtanjica'*, Co = *Colveraia*, Eo = *Eodictyoptychus*, Se = *Semailia*, Di = *Dictyoptychus*, Pl = *Plagioptychus*, Pi = *Pironaea*, Vl = *Vaccinites loftusi*, Vv = *Vaccinites vesiculosus*, Vo = *Vaccinites oppeli*, Hc = *Hippurites cornucopiae*, H = *Hippurites* aff. *lapeirousei*, T = *Torreites*.

DESCRIPTION. All four specimens have the valves conjoined, with the upper left valve slightly exogyriform and the lower valve rather longer but with considerable variation in size of attachment surface; line of commissure slightly sinuous. Outer shell surface of both valves with fine, evenly and closely spaced, radiating striiform ribs. Shell margins crenulate. Adductor attachments visible in the left valve of specimen LL41767 on concave surfaces of the hinge plate, a little below the plane of commissure. *Gyropleura* is a clinger.

Family **PLAGIOPTYCHIDAE** MacGillavry, 1937: 105, 152
(*ex*. Plagioptychinae MacGillavry, 1937 (plagioptychinés Douvillé, 1888: 729))
Genus ***PLAGIOPTYCHUS*** Matheron, 1843.

TYPE SPECIES. *Plagioptychus paradoxus* Matheron, 1843, subsequently designated by Kutassy (1934: 172).

REMARKS. Species of *Plagioptychus* are clingers to low elevators.

Plagioptychus* cf. *toucasianus Matheron, 1843 Pl. 1, fig. 1

cf. 1843 *Plagioptychus toucasianus* Matheron, 117.

MATERIAL. Two small specimens from near the base of the Simsima Formation at Jebel Faiyah, BM LL41765 (centre), LL41766 (from section 2), Skelton Collection.

DESCRIPTION. Inequivalve, right valve smaller than free left valve, exogyriform with sinuous commissural margin with large attachment area, surface slightly rugose with prominent commarginal growth lines. The rather short exterior dorsal surface has a sub-vertical ligament groove and the shell surface bulges to the posterior of this line. Outer calcitic shell layer thin to medium, with thin inner layer without pallial canals. Prominent tooth and attached myophore projects into upper valve.

Free left, upper valve globose, regularly coiled, gryphaeate with smooth surface; outer calcitic shell layer thin, inner layer recrystallized to calcite but medium to thick, with radially elongated narrow canals that do not pass into polygonal structure and in that way differ from *Mitrocaprina* or the upper valve of *Coralliochama*. The narrow canals also do not bulge internally as is common in some forms of the genus. Anterior myophore robust and nearly level with the commissure. An oblique septum runs from the anterior tooth to the ventral margin. The cavity posterior to this septum houses the large central tooth and conjoined posterior myophore in a dorsal position.

Family **DICTYOPTYCHIDAE** Skelton *in* Skelton & Benton, 1993
(*ex*. Trechmannellidae Cox, 1933: 65)

DIAGNOSIS. Inequivalved rudists, attached by right valve. Valves uncoiled and ligament absent. Outer (calcitic) shell layer compact. Inner (originally aragonitic) shell canaliculate throughout, in both valves. Two projecting teeth in left valve, straddling ridge-like central tooth in right valve. Posterior tooth dorso-ventrally flattened, flanking body-cavity, and separated from the dorsal margin by a small accessory cavity, which may be a relic of the ligamentary cavity. Anterior myophoral platforms extended both dorsally on hinge plate, around anterior tooth, and ventrally from hinge plate. Posterior myophore of left valve projecting, with adductor scar facing outwards, into recess, or socket, in posterior wall of right valve, and directly flanking body-cavity.

REMARKS. The distinctive features of this family were discussed, in relation to *Eodictyoptychus*, by Skelton and El-Asa'ad (1992). The dictyoptychid myocardinal apparatus differs from that seen in the Caprinidae (s.s.), the Plagioptychidae, and *Sabinia* (s.s.) in all of which the posterior tooth and posterior myophore (with *inward*-facing muscle scar) of the left valve are separated from the body-cavity by the combined central tooth socket and an accessory cavity, extending ventrally from it, which receives the salient myophore of the right valve. The latter cavity is itself demarcated by a prominent lamina running from the anterior tooth to the postero-ventral margin of the valve. No equivalents of this lamina, and the associated accessory cavity, are present in the left valve of dictyoptychids.

Pseudosabinia (Radiolitidae) differs in its possession of a

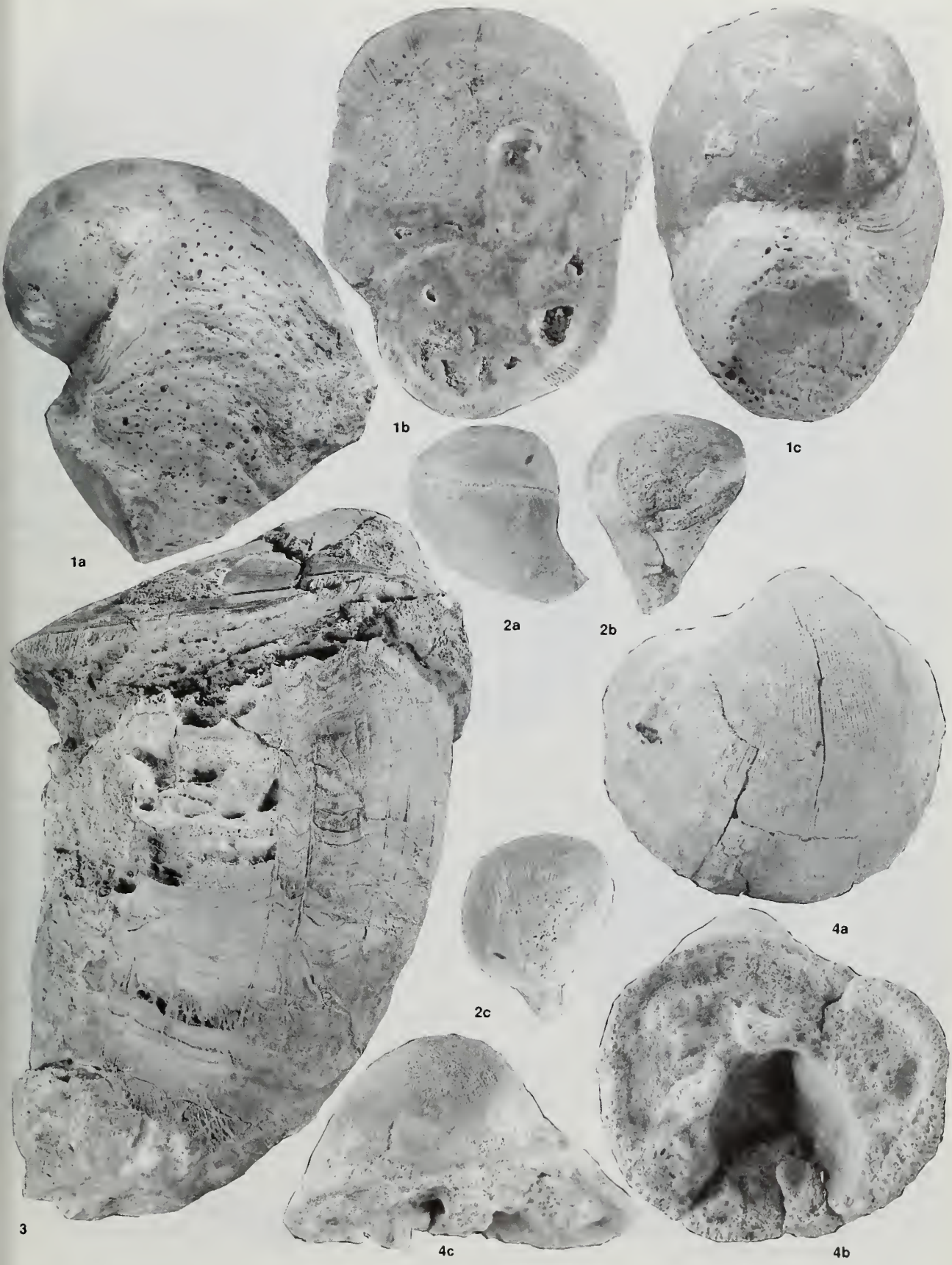
PLATE 1

Fig. 1 *Plagioptychus* cf. *toucasianus* Matheron, from Jebel Faiyah, lower part of Simsima Formation. **1a**, anterior view, **1b**, section through left valve approximately 5 mm from the commissure, BM LL41766, × 1, Skelton Collection **1c**, dorsal view, BM LL41765, × 1.

Fig. 2 *Gyropleura* sp., from Jebel Rawdah, section 1, loose from top of bed 2 or bed 3 of Simsima Formation; **1a**, posterior view, **1b**, dorsal view, **1c**, view looking down on left valve, BM LL41768, × 2.

Fig. 3 *Dictyoptychus morgani* (Douvillé), from Jebel Buhays, section 1, bed 11 of Simsima Formation, side view, BM LL41680, × 0·5.

Fig. 4 *Eodictyoptychus arumaensis* Skelton & Al-Asa'ad, from Jebel bu Milh, section 1, top of Qahlah or basal Simsima Formation; **4a**, top view, **4b**, internal view, **4c**, dorsal view, BM LL41927, left valve, × 1·5.


1a
1b
1c
2a
2b
2c
3
4a
4b
4c

ligamentary invagination, and the presence of cellulopris-matic structure in the outer shell layer of the right valve. Despite the similarity to the Antillocaprinidae MacGillavry, 1937, in their lack of a ligament, and the presence of the small dorsal accessory cavity, which may be a relic of it, the dictyoptychids differ from *Antillocaprina* (at least) in having the posterior myophore of the left valve projecting, rather than parallel with the plane of commissure. Moreover, the outer shell layer of antillocaprinids is invariably very thin, whilst that of dictyoptychids is usually relatively thick in the right valve.

Genus ***DICTYOPTYCHUS*** Douvillé, 1905.
(*nom. nov.* for *Polyptychus* Douvillé 1904, *non* Huebner, 1816)

TYPE SPECIES. *Polyptychus morgani* Douvillé, 1904, by monotypy.

SYNONYM. *Trechmannella* Cox, 1933 (obj.).

REMARKS. Attached right valve with large polygonal canalicular structure. Outer layer of right valve thicker than that of left valve, with exposed growth margin; sharply peaked ridges on right valve growth margin in some specimens. We agree with Pons *et al.*, 1992, who regard all described species as probably synonymous.

Dictyoptychus morgani (Douvillé, 1904) Pl. 1, fig. 3

1904 *Polyptychus morgani* Douvillé: 248–51, pl. 33 bis.
1905 *Dictyoptychus morgani* (Douvillé); Douvillé: 198.

MATERIAL. Jebel Faiyah, section 1, bed 3, BM LL41670–71; section 2, LL41659; Jebel Faiyah, centre, LL41683–84. Jebel Aqabah, Simsima Formation, loose, BM LL41676. Jebel Thanais, Simsima Formation, loose in scree, BM LL41668–69. Jebel Buhays, section 1, bed 11, LL41677, 41680; section 1b, LL41674; section 1a, Simsima Formation, BM LL41675. Jebel Rawdah, section 1, bed 3, BM LL41657–58, 41679, 41681; section 2, bed 19, LL41673; section 2, loose on scree, LL41667; section 4, bed 1, LL41672; Jebel Rawdah, north, LL41690. Jebel Bu Mihl, section 1, bed 3, BM LL41660–66. Jebel Huwayyah, section 2, beds 3–5, BM LL41678; Jebel Huwayyah, LL41685–89. Jebel Sa'ah, basal Simsima Formation, BM LL41682.

REMARKS. Occurs widely in the lower half of the Simsima Formation, sometimes in great numbers. *Dictyoptychus* is a multigeniculate elevator (see Ross & Skelton, 1993: fig. 5.2).

Genus ***EODICTYOPTYCHUS*** Skelton & El-Asa'ad, 1992

TYPE SPECIES. *Eodictyoptychus arumaensis* Skelton & El-Asa'ad, 1992, by original designation.

Eodictyoptychus aff. ***arumaensis*** Skelton & El-Asa'ad, 1992. Pl. 1, fig. 4; Pl. 2, fig. 2

v aff. 1992 *Eodictyoptychus arumaensis* Skelton & El-Asa'ad: 108–13, pl. 1, figs 1–6.

MATERIAL. Jebel Bu Milh, section 1, Qahlah/Simsima Formation Boundary, BM LL41927–8; section 2, LL41929; all are left valves. A possible fragment of a right valve from Qarn Murrah, BM LL41977, Skelton Collection.

DESCRIPTION. Moderately inaequivalved, free left valve with thin outer calcitic shell layer, inner aragonitic layer recrystallised but formed of varyingly sized canals of polygonal section, even within the teeth and the massive myophores. Two subequal, projecting teeth in free valve, the anterior one below the umbo, the smaller, posterior one ventral to this, the two separated by a socket whose centre lies above and towards the umbo from the posterior tooth. The teeth lie on the body-cavity side of a massive plate which includes the attachment surfaces of the myophores, and takes up more than half of the area within the valve when looking down on the commissural plane.

We have not been able to detect the accessory cavity dorsal to the posterior tooth, but this may be due to the difficulty of its preparation. The projecting posterior myophore is separated from the body-cavity by a narrow ledge which is not present in the type material from Khashm Buwaibiyat, approximately 50 km north of Riyadh.

REMARKS. *Eodictyoptychus* varies from a lateral clinger to a recumbent.

Genus ***SEMAILIA*** Morris & Skelton, gen. nov.

TYPE SPECIES. *Semailia smithi* Morris & Skelton gen. et sp. nov.

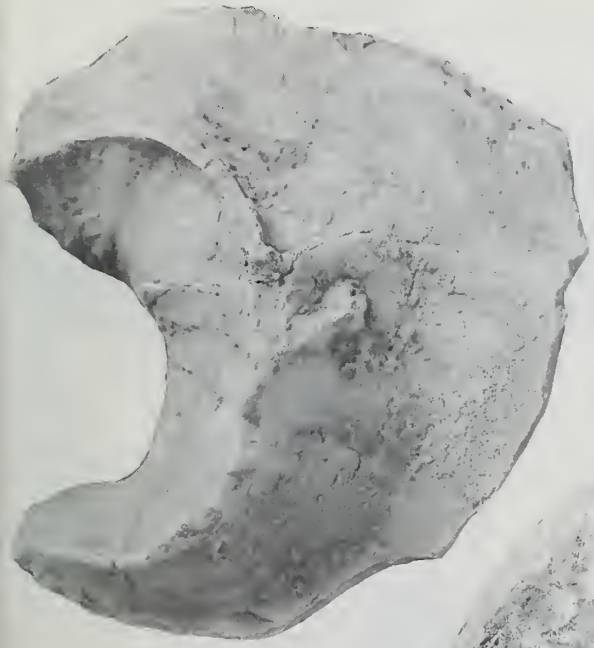
DIAGNOSIS. Bicornate and multicarinate, subequivalve with a thin outer shell layer in each valve. Inner shell canaliculate in both valves. Myocardinal arrangement typical of dictyoptychids with two teeth in the left valve, the posterior tooth dorso-ventrally flattened and flanking the body-cavity without an intervening accessory cavity. No ligament present. The posterior myophore of the left valve projecting into a socket in the right valve, again flanking the body-cavity without an intervening accessory cavity.

REMARKS. The absence of a posterior accessory cavity in the left valve excludes this taxon from the Caprinidae, Plagioptychidae and *Sabinia* s.s., and the outward facing, ie monopleuriform, myophores, are typical of the dichtyoptychid plan. Unlike other members of the Dictyoptychidae this genus does not show the differentially greater thickening of the outer calcitic layer of the right valve.

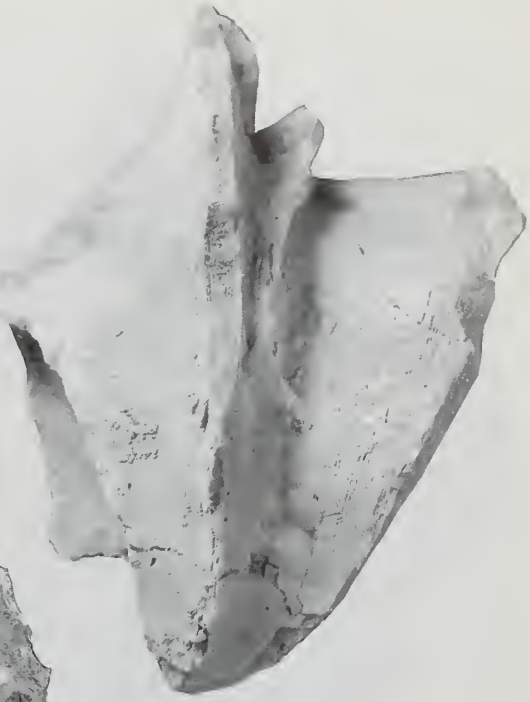
PLATE 2

Fig. 1 *Semailia smithi* Morris & Skelton, gen. & sp. nov. Jebel Huwayyah, section 2, *Loftusia*-Beds; **1a**, anterior view, **1b**, posterior view, **1c**, view of right valve, **1d**, dorsal view; holotype, BM LL41931, × 1.

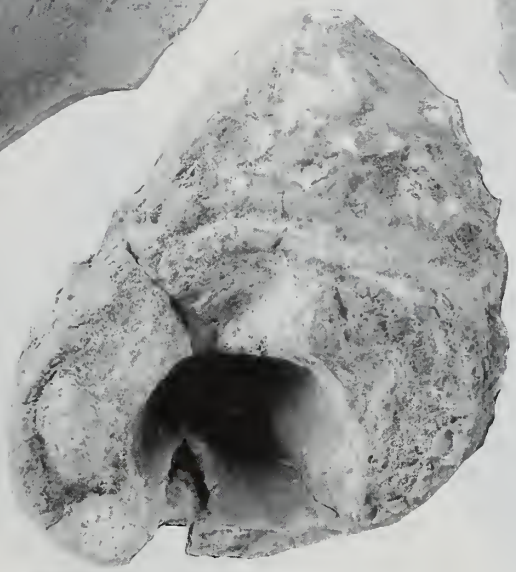
Fig. 2 *Eodictyoptychus aff. arumaensis* Skelton & Al-Asa'ad, Jebel bu Milh, section 1, top of Qahlah or base of Simsima Formation; internal view of left valve, BM LL41928, × 1.



1a

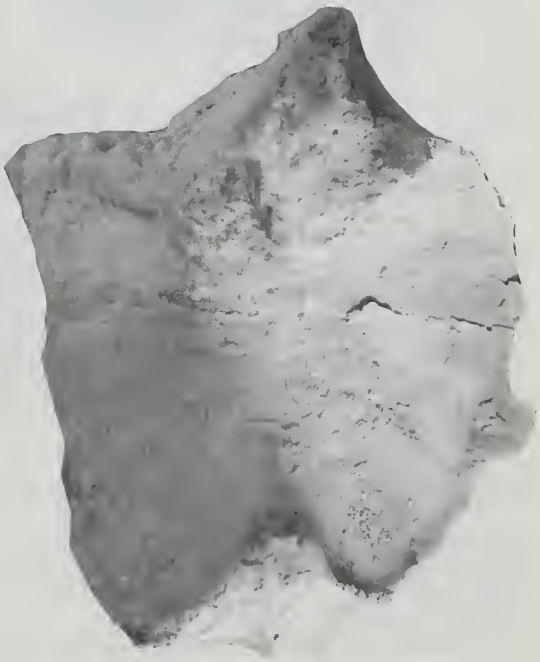


1c



2

1b



1d

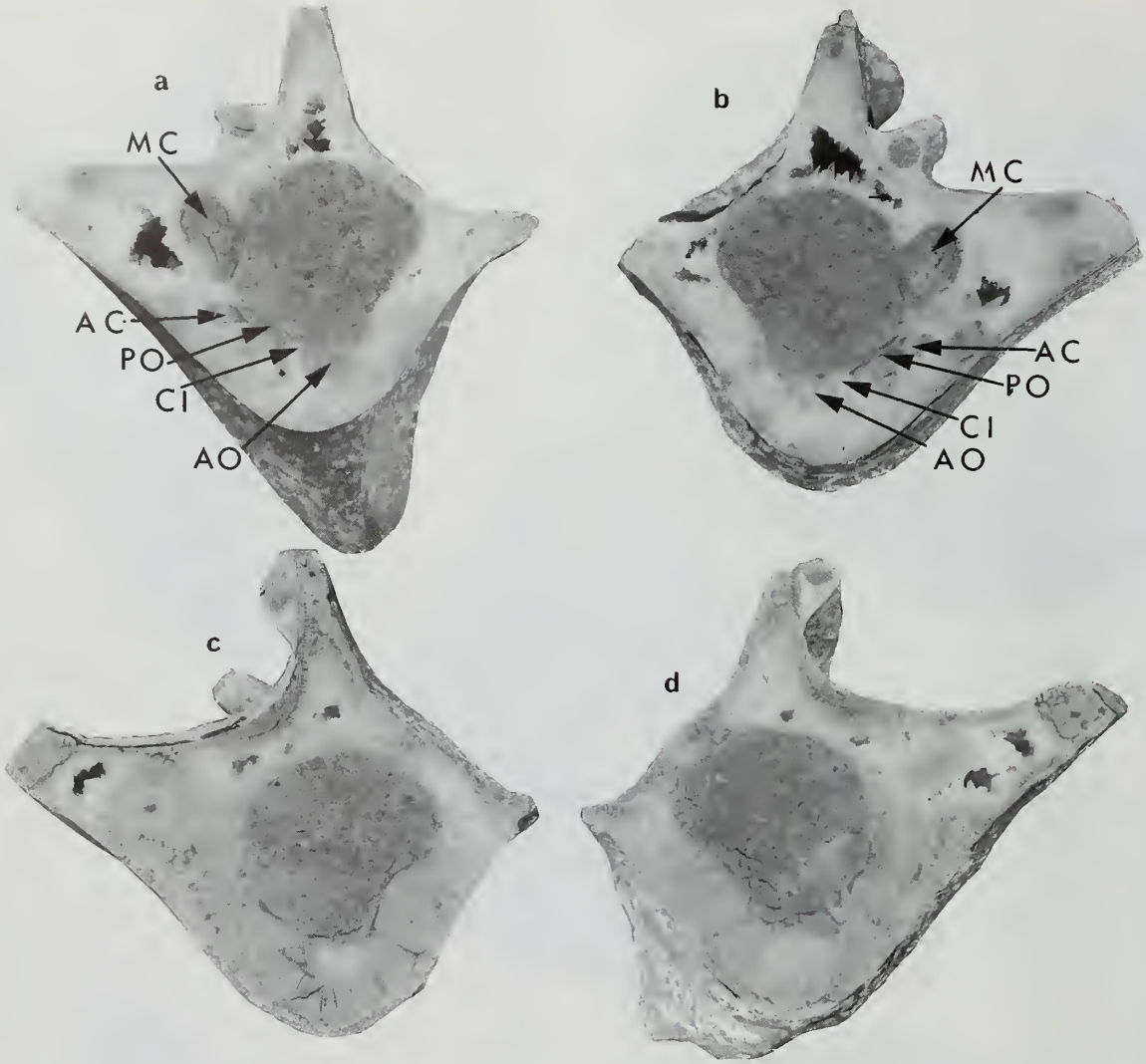


Fig. 3 *Semailia smithi* Morris & Skelton sp. nov. Four sections through the holotype approximately 10 mm either side of the commissure, BM LL41931; **a, b**, right valve, MC – accessory cavity for posterior myophore of left valve, PO – posterior tooth socket, AC – accessory cavity dorsal to tooth socket, CI – central tooth, AO – anterior tooth socket; **c, d**, left valve, with fine outer and large irregularly polygonal inner canals; × 1.

PLATE 3

Fig. 1 *Semailia* sp., Jebel bu Milh,section 2, base of Simsima Formation; **1a**, ventral view of broken right valve, **1b**, dorsal view of right valve; BM LL41932 × 0·75.

Fig. 2 *Torreites sanchezi milovanovici* Grubić; Haushi-Huqf Massif, Eastern Oman, BM LL41975, Samir Hanna Collection; **2a**, view looking down onto commissural plane with broken left valve partly preserved in situ, × 1; **2b**, dorsal view showing intucking of pillar L, **2c**, posterior view showing infolds of pillars, **2d**, ventral view; 2b–d, × 0·5.

Fig. 3 *Vaccinites* aff. *oppeli* (Douvillé), Jebel bu Milh, section 2, Simsima Formation, bed 10, BM LL41730, marginal surface of outer shell layer of right valve, × 1.

Semailia smithi Morris & Skelton sp. nov. Pl. 2, fig. 1, Fig. 3

MATERIAL. A single specimen, the holotype, BM LL41931, from Jebel Huwayyah, section 2, *Loftusia*-Beds.

DIAGNOSIS. Typical of the genus but with three strong carinae or flaring radial costae on each valve.

DESCRIPTION. Both valves are preserved, closed, although the body-cavity is matrix-filled and includes larger foraminifera. The specimen has two serpulids attached, one to each valve and aligned radially with respect to the umbones, with their apertures close to the valve commissure, amid the plicae of the ventral margins.

The shell is curvingly biconical, with the two valves separately following almost a semicircular direction of growth, in


1a
2a
1b
2d
2b
2c
3

a single plane, so that the umbones or apices are beginning to approach each other; sub-equivalve with the right valve slightly 'longer' than the left. Three prominent carinae or flaring radial costae, skewed to the posterior, two at approximately 180°, set anteriorly and posteriorly on both valves and the third normal to these on the ventral margin. Dorsal margin rounded. Shell surface otherwise relatively smooth on both valves.

No ligament present. Very thin outer calcitic shell layer in both valves. Canals are present in the thick inner shell layer of both valves, round and capillary-like around the margins, becoming larger inside, irregularly rounded polygonal in section, especially in the left valve.

Two teeth in the left valve are typical of the family, the anterior one is rounded and knob-like, the posterior one is dorso-ventrally flattened. One central tooth in the right valve. The posterior myophore of the left valve projects into an accessory cavity (socket) in the right valve. The anterior myophore of the left valve is a broad shelf and has large canals. There is an accessory cavity in the right valve which lies dorsally to the flattened posterior tooth socket.

COMMENTS. The crescentic form of the shell suggests a recumbent life position, possibly reclining on the dorsal flank. It was found in a matrix of marly limestones with large specimens of *Loftusia* with a similar matrix filling the body-chamber, forming a loftusid packstone.

COMPARISON WITH OTHER TAXA. There is a great similarity in the myocardinal arrangement with that of other dictyoptychids, but *Semailia* differs in having a much thinner outer shell layer in both valves and having strong shell carinae.

Semailia sp. Pl. 3, fig. 1

MATERIAL. A single specimen from Jebel Bu Milh, section 2, basal Simsima Formation, BM LL41932.

DESCRIPTION. The specimen is a large right valve, its anterior and posterior part nearly symmetrical about a dorso-ventral plane. Multicarinate but otherwise smooth. Two wide anterior and posterior carinae form a wide kite-shape in dorsal view. Dorsal surface flattish near the commissure, but umbones incurved and separating two gently concave anterior and posterior areas with a low mid-dorsal carina that is prominent at the umbo, but faces towards the mid-dorsal margin. Ventral part of shell has three sub-equal strong carinae, which are equidistant from the dorsal margin and inclined towards the anterior.

Outer shell layer thin and now formed of structureless recrystallized blocky calcite. Thick canaliculate inner shell layer with capillary-like polygonal canals throughout, including the teeth, fine at the margins becoming larger inwards, now also recrystallized to calcite.

Right valve has part of projecting stout central tooth preserved behind base of the socket for the anterior tooth of the left valve and in front of the socket of the posterior tooth of the left valve, containing a fragment of that dorso-ventrally flattened tooth.

COMPARISON WITH OTHER SPECIES. *Semailia* sp. differs from *S. smithi* in having two additional ventral carinae. There is not enough material to know if this difference is significant in discriminating separate species.

Family **HIPPURITIDAE** Gray, 1848
Subfamily **TORREITINAE** Grubić, 1980
Genus ***TORREITES*** Palmer, 1933

TYPE SPECIES. *Hippurites (Vaccinites) sanchezi* Douvillé, 1927, by original designation.

DESCRIPTION. Outer shell layer of right valve with tight marginal infoldings, giving rise to radiating crests (Douvillé, 1894) around the shell margin of the right valve, but variable in extent and number. Outer shell layer of left valve thin, postero-dorsally digitiform, smooth except for fine growth lines on the upper surface, but becoming overgrown with epibionts radiating from its low apex. Inner shell layer of both valves partly canaliculate, canals of right valve relatively large, sub-radial and sub-rectangular in section, in the area of the anterior muscle attachment. We have observed a similar reticulate network of vertical ridges separating tabulate canals in the anterior myophoral ledge of *Vaccinites gosaviensis* (BM 33972, a specimen with the original aragonite preserved). The canals of the left valve are narrow and radiate from the apex.

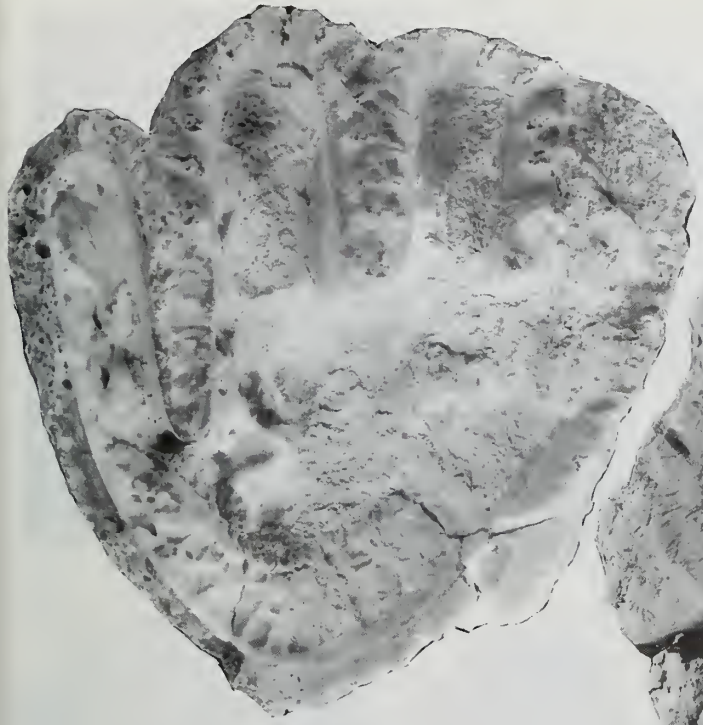
REMARKS. Philip & Platel (1994) pointed to the similarity of *Torreites* with their new genus, *Praetorreites*, from the Lower Campanian, Samhan Formation of south-east Oman. The latter has canaliculate structure of the inner shell layer of the left valve and regular pedunculate radial structures in the outer shell layer of the right valve, which, they claim, are comparable with the radiating marginal crests of *Torreites*. They compare the subfamily, raised to family rank, with both the Plagioptychidae and the Hippuritidae, concluding that the similarity is greater with the Plagioptychidae. If Philip & Platel are correct in their suggestion that the Torreitinae are not hippuritids, then it follows that the three large infolds of the outer shell layer of the right valve are not homologues of the hippuritid pillars. The origin of two of the pillars of *Torreites* is claimed to be from the two small 'pillars' of *Praetorreites* and considered by Philip & Platel to be analogues of pillars 'E' and 'S'. Philip & Platel's plate 8, fig. 1 shows the position of these 'pillars' in relation to the teeth and myophores of the upper valve. If this arrangement is compared with the hinge structures of *Dictyoptychus* (Douvillé, 1904: pl. 33 bis, fig. 4), the alignment of the sockets and teeth is very similar, although they are at a more obtuse angle

PLATE 4

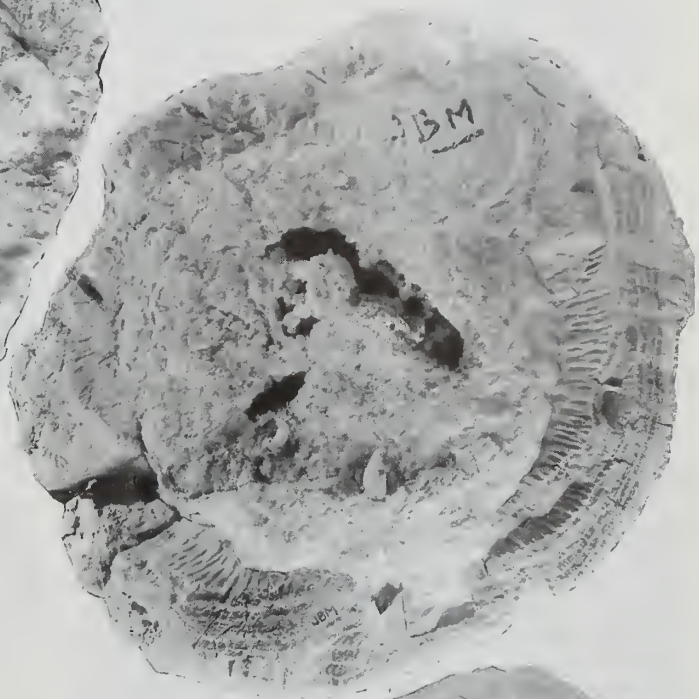
Fig. 1 *Torreites sanchezi milovanovici* Grubić, Haushi-Huqf Massif, Eastern Oman (also figured Skelton & Wright, 1987: pl. 67, fig. 1), BM LL28004, view looking down onto right valve (note coarse cellular structure of myophore in lower part of figure and tooth sockets to the right of pillar 'L'), × 1.

Fig. 2 *Vaccinites* aff. *oppeli* (Douvillé), Jebel bu Milh, section 2, Simsima Formation limestone, BM LL41733, view of naturally broken section of right valve, × 0·4.

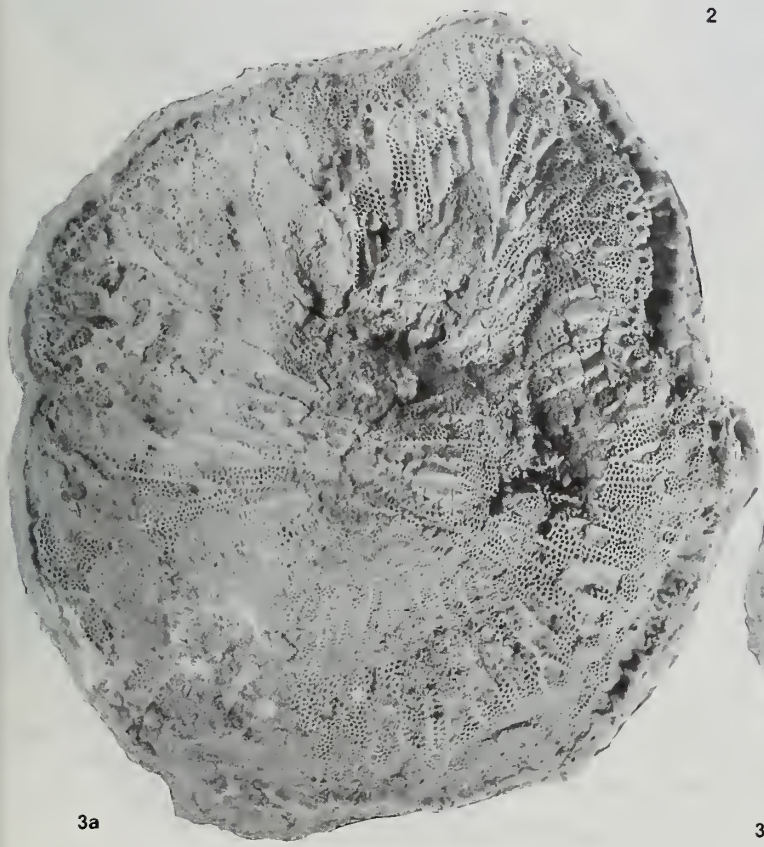
Fig. 3 *Vaccinites vesiculosus* (Woodward), Jebel Huwayyah, *Loftusia*-Beds, BM LL41716, Skelton Collection, **3a**, view of partly eroded left valve, **3b**, view of right valve, × 0·5.



1



2



3a

3b

to the ventral shell margin. This suggests a relationship between *Dictyoptychus* and *Praetorreites*.

It is difficult to relate the anterior infolding of *Torreites* to the position of ligamentary invagination of the plagioptychids, but much easier if *Torreites* is interpreted as a hippuritid. Details of the morphology are illustrated by Skelton & Wright (1987: fig. 2). In Skelton & Wright's interpretation of *Torreites* loss of the hippuritid canal system of the outer shell layer of the left valve is by recurvature of the shell margin to expose the mantle margins. The umbo of the operculiform left valve is close to the ventral margin.

Philip & Platel (1994: fig. 4) claim a diphyletic origin for the 'three-pillared' genus *Torreites* and thus claim to have refuted the palaeobiogeographical interpretation of Skelton & Wright (1987). Their diagram shows *Praetorreites* occurring before *Torreites* and giving rise independently to the Caribbean and Arabian species. However, their date for the small Caribbean species *Torreites tschoppi* on this diagram does not show its full range. There is ample evidence to show that this species is best dated as Santonian in Cuba (Rojas *et al.*, *in press*) and therefore pre-dates Campanian *Praetorreites*. Their analysis leading to the view that the torreitines are not closely related to the hippuritids relies heavily on the interpretation of the ancestral status of *Praetorreites* and the supposed homology of the pedunculate folds, with the marginal radiating crests of *Torreites*, which in the latter are a consequence of tight infoldings of the outer shell surface. A superficially similar structure in section may be seen in the outer shell layer of the lower valve of *Dictyoptychus striatus*, but this is formed as a consequence simply of salient radial ridges on the growth margin of that shell layer, without any infolding of the outer surface. In Philip & Platel's (1994: pl. 7, fig. 3) illustration of *Praetorreites* the similarity, if anything, seems greater with the radial ridges of the dictyophychid, than with the intuckings of *Torreites*. In all particulars *Praetorreites* is similar to *Eodictyoptychus* and appears to have little in common with *Torreites*.

The criticism of Skelton and Wright's (1987) explanation of the distribution of *Torreites* is therefore unconvincing. We maintain the view that the differences between the Caribbean and Arabian *Torreites* do not warrant greater that subspecific separation, and that their similarities do reflect that genetic interchange between the two areas of occurrence did take place.

Fig. 4 *Torreites sanchezi milovanovici* Grubić; smooth top surface of left valve with advancing front of epibionts (arrowed), BM LL41975, × 2.

Fig. 5 Camera lucida drawing of *Vaccinites loftusi* (Woodward); from Qarn Murrah, BM LL41933, Skelton Collection, × 1.

Torreites sanchezi (Douvillé, 1927), subsp. *milovanovici* Grubić, 1980

Pl. 3, fig. 2; Pl. 4 fig. 1

1927 *Hippurites (Vaccinites) sanchezi* Douvillé: 54, 55, pl. 4, fig. 1.

1980 *Torreites milovanovici* Grubić: 92, 93, pl. 1, fig. 1, fig. 4.

PLATE 5

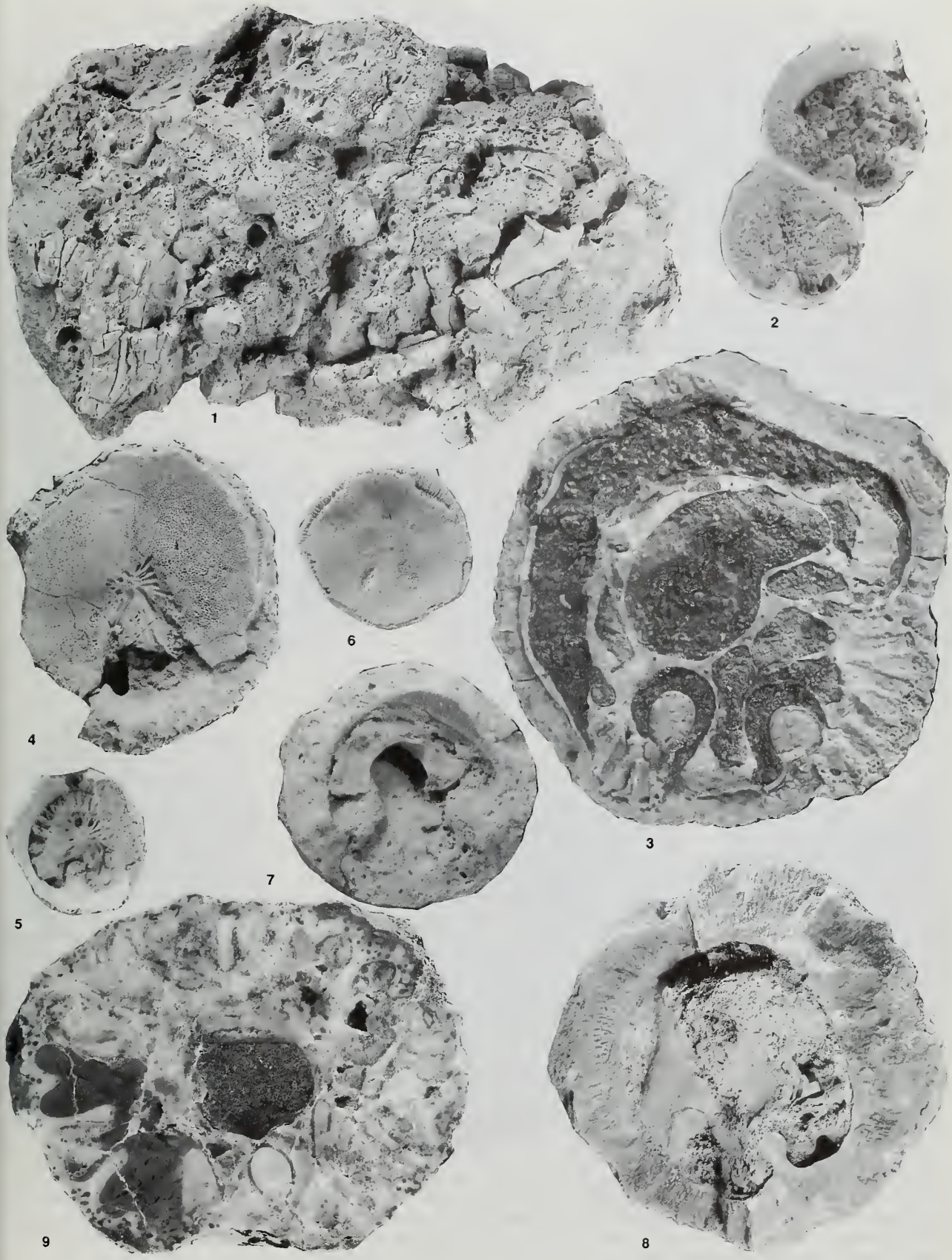
Figs 1, 2 *Hippurites* aff. *lapeirousei* Goldfuss; **1**, Jebel Faiyah, section 1, Simsima Formation, bed 6, BM LL41754, mass of variously orientated individuals, × 0·5; **2**, Jebel Faiyah, section 1b, Simsima Formation, bed 2, BM LL41755, view looking down onto a pair of right valves, × 2.

Fig. 3 *Vaccinites vesiculosus* (Woodward), Jebel Huwayyah, *Loftusia*-Beds, BM LL41973, V. Chalmers Collection, view looking down on eroded left valve exposing pillars of right valve, × 1.

Figs 4–7 *Hippurites cornucopiae* Defrance; **4–6**, Jebel Faiyah, loose from low in the Simsima Formation, Skelton Collection; **4**, BM LL41747, view of left valve (pores appear polygonal and radially vermiculiform where less eroded), × 1; **5**, BM LL41744, eroded left valve showing pores and canals, × 1; **6**, BM LL41745, view of left valve with oscules and pores appearing vermiculiform or polygonal depending on the degree of erosion, × 1; **7**, BM LL41737, Jebel Thanais, natural section through right valve showing slightly pedunculate pillars, × 1.

Fig. 8 *Hippurites* aff. *cornucopiae* Defrance, Jebel Rawdah, southern flank, loose from Simsima Formation, BM LL41753, Skelton Collection, natural section of right valve, × 0·5.

Fig. 9 *Pironaea* cf. *polystyla* Pirona, Qarn Mulayh, BM LL41938, Skelton Collection, section through right valve, × 1.


1
2
3
4
5
6
7
8
9

1994 *Torreites milovanovici* Grubić; Philip & Platel: pl. 8, fig. 4, fig. 4.
(For further synonomy see Skelton & Wright, 1987)

TYPE SPECIMEN. The holotype of the subspecies is BM LL27699, Iraq Petroleum Company Collection (CP 86), on weathered surface of section, 7·7 m from top at Qarn Mulayh.

OTHER MATERIAL. Two specimens from the same horizon on Qarn Murrah, BM LL41761, 62; a well-preserved specimen showing details of the upper valve, from the Haushi-Huqf Massif, eastern Oman, S. Hanna Collection, BM LL41975; the material of Skelton & Wright (1987) from eastern Oman, BM LL28004; one specimen from Jebel Huwayyah, section 1, Qahlah gravels, BM LL42763; Qarn Mulayh, no specimens collected.

COMMENTS. BM LL41975 shows a boundary between shiny outer shell material and encrusted surface on the outer surface of the upper valve which we interpret as representing the limit of encroachment upon the exposed left mantle surface by epibionts. BM LL28004 shows the loose canalicular structure of the anterior muscle attachment area of the right valve together with the tooth sockets.

Subfamily HIPPURITINAE Gray, 1848
Genus ***VACCINITES*** Fischer, 1887

TYPE SPECIES. *Hippurites cornuvaccinum* Bronn, 1931, by monotypy.

Vaccinites loftusi (Woodward, 1855) Fig. 5

1855 *Hippurites loftusi* Woodward: 58, pl. 3 figs 2–3.
1897 *Hippurites loftusi* Woodward; Douvillé: 210, pl. 33 (17), figs 1, 1a, 1b.
1904 *Vaccinites loftusi* (Woodward); Toucas: 82, 83, figs 126, 127.

MATERIAL. Three specimens from Qarn Murrah, BM LL41933, LL41969–70; another from Jebel Huwayyah, *Loftusia*-Beds, LL41934; Skelton Collection.

REMARKS. These specimens have the typical coarse external ribs of Woodward's species but are very poorly preserved internally. The pillars of a Qarn Murrah specimen resemble those of Woodward's type but were not enhanced by sectioning. The pores of the upper valve are in the form of coarse polygons and the outer surface of this left valve has radial undulations. Woodward's type material has incipient multiple infoldings of the outer shell layer of the right valve, reminscent of *Pironaea*.

Vaccinites vesiculosus (Woodward, 1855) Pl. 4, fig. 3; Pl. 5, fig. 3

1855 *Hippurites vesiculosus* Woodward: 59, pl. 4, fig. 6.
1897 *Hippurites vesiculosus* Woodward; Douvillé: 201, pl. 29 (13), figs 6, 7.
1904 *Vaccinites vesiculosus* (Woodward); Toucas: 110, 111.

MATERIAL. Qarn Murrah, BM LL41691–7, LL41721–26, Skelton Collection; Jebel Huwayyah, section 1, bed 9, BM LL41698–702; section 2, bed 7 (the main coral bed), BM LL41703–4; section 2, beds 2–7, BM LL41705–15 plus another 9 specimens; Jebel Huwayyah, loose, Skelton Collection, BM LL41716–20, V. Chalmers Collection, BM LL41973; three possible specimens from Jebel Thanais, loose in scree below lowest 3m of the Simsima Formation, BM LL41935–37.

REMARKS. The specimens from the *Loftusia*-Beds at Jebel Huwayyah are larger than either those from Qarn Murrah or Woodward's type material. They however have the same type of pillars in the right valve with a long thin arête cardinal and pedunculate pillars. The complex pattern of the canals and pores of the left valve are also similar in each of the three groups of material. *V. vesiculosus* is the dominant rudist species in the *Loftusia*-Beds at Jebel Huwayyah.

Vaccinites* aff. *oppeli (Douvillé, 1892) Pl. 3, fig. 3; Pl. 4 fig. 2

aff. 1866 *Hippurites dilatatus* Defrance; Zittel: 142, pl. 24, figs 1–5.
aff. 1881 *Hippurites zitteli* Munier-Chalmas *in* Zittel: 83, fig. 118 (*non* Matheron, 1880).
aff. 1892 *Hippurites oppeli* Douvillé: 36, 37, figs 23, 24, pl. 4 (18), fig. 5.
aff. 1897 *Hippurites oppeli* Douvillé: 203, pl. 31 (15), figs 1, 1a.
aff. 1904 *Vaccinites oppeli (Douvillé); Toucas: 109, 110, pl. 17 (18), figs 2, 2a.*

MATERIAL. Jebel Bu Mihl, section 2, common, many may be in life position, lower part of the main Simsima Limestone, BM LL41728–30, 41733; Hill to south of Jebel As-Saifr (east of Jebel Huwayyah), BM LL41731–32, Skelton Collection.

REMARKS. In this very large form, the pores of the upper valve are present in one specimen and are similar to the pore system in topotypic material from Gosau, particularly on the outer third of the radius. The outer shell surface is rather smooth. The raised pattern on the growth surface of the outer shell layer of the right valve is extremely similar to the Austrian material (cf. Zittel, 1866: fig. 1). The pillars in the right valves of our material match very closely with those of

PLATE 6

Fig. 1 *Durania* Form A, Jebel Huwayyah, section 1, from the Qahlah gravels, BM LL41948, part of outer shell layer of right valve with concave smooth dorsal radial band to the right, × 1.

Fig 2 *?Radiolites* sp., Jebel bu Milh, section 2, beds 7/8 at the Qahlah/Simsima boundary, BM LL41947, right valve, **2a**, view of interior, **2b**, ventral view, **2c**, anterior view; all × 1·5.

Figs 3, 4 *Praeradiolites* cf. *subtoucasi* Toucas, Jebel Rawdah, section 4, bed 1, basal rudist bed of Simsima Formation; **3**, BM LL41941, section across lower part of right valve, × 1; **4**, BM LL41942, view of anterior of right valve, × 1.

Fig. 5 *Pseudopolyconites* aff. *parvus* Milovanović, Qarn Mulayh, BM LL41974, Skelton Collection, × 1; **5a**, section through right valve with arête cardinale at top; **5b**, surface of part of right valve with smooth ventral radial band centre and sediment with spines to right.

Fig. 6 *Durania* cf. *apula* Parona, Jebel Rawdah, section 2, Simsima Formation, bed 10, BM LL41951; **6a**, ventral view of right valve showing radial bands; **6b**, part of upper surface of right valve with small holes near the radial bands, × 1.


1
2a
2b
2c
3
4
5a
5b
6a
6b

the Austrian material. The differences seem to relate only to phyletic size increase.

Genus ***HIPPURITES*** Lamarck, 1801

TYPE SPECIES. *Hippurites bioculatus* Lamarck, 1801, by monotypy.

Hippurites* aff. *lapeirousei Goldfuss, 1841 Pl. 5, figs 1, 2

aff. 1895 *Hippurites lapeirousei* Goldfuss; Douvillé: 164, pl. 24 (11), figs 7–10.
aff. 1903 *Orbignya lapeirousei* Goldfuss; Toucas: 53, pl. 6 (12), figs 10, 11.

MATERIAL. Jebel Faiyah, Sharjah, section 1a, bed 6, BM LL41754; section 1b, bed 2b, BM LL41755; Jebel Faiyah, loose, BM LL41758, Skelton Collection; Jebel Rumaylah, BM LL41756, Skelton Collection; Jebel Mundassah, BM LL41757, Skelton Collection.

REMARKS. This species is present in large masses of disorientated specimens close to coral patches, low in the Simsima Formation at Jebel Faiyah. It has broad and short pillars and lacks an arête cardinale. It differs from typical specimens from Maastricht in having a rather smooth shell surface to its right valve.

Hippurites cornucopiae Defrance, 1821 Pl. 5, figs 4–7

aff. 1821 *Hippurites cornucopiae* Defrance: 195, pl. 58, figs 1a, 1b (only).
1910 *Hippurites (Hippuritella) cornucopiae* Defrance; Douvillé: 79, pl. 7, figs 3–5.

MATERIAL. Jebel Faiyah, section 1, BM LL41735; Jebel Faiyah, loose, BM LL41738, 41744–47, Skelton Collection; Jebel Buhays, section 1, bed 15, BM LL41739–43; section 3, BM LL41736; Jebel Thanais, BM LL41737, Skelton Collection; Jebel Rawdah, section 2, BM LL41734.

REMARKS. The pores of the upper valve, together with the disposition and shape of the pillars of the lower valve, match those described by Douvillé from Sicily, which is the type locality of Defrance's species. However, although the pores are polygonal and denticulate even when the surface is only slightly eroded, they are radially vermiculiform when the outer surface is intact. Hence the species should be assigned to *Hippurites* not *Hippuritella* (*pace* Douvillé, 1910). Rather conical specimens occur at the coral patch horizon at Jebel Faiyah, sometimes within the coral clumps.

Hippurites* aff. *cornucopiae Defrance, 1821 Pl. 5, fig. 8

MATERIAL. Jebel Faiyah, BM LL41750, LL41752, Skelton Collection; Jebel Rawdah, section 3, above Simsima conglomorate, BM LL41748; Jebel Rawdah, loose, BM LL41749, 41751, 41753, Skelton Collection.

REMARKS. Specimens from Jebel Faiyah and Jebel Rawdah that occur well up the sequence of the Simsima Formation are of Upper Maastrichtian age. They are similar in general plan to *H. cornucopiae* but are much larger, always being more than twice the diameter of the latter.

Genus ***PIRONAEA*** Meneghini *in* Pirona, 1868

TYPE SPECIES. *Hippurites polystylus* Pirona, 1868, p. 511.

Pironaea* cf. *polystyla Pirona, 1868 Pl. 5, fig. 9.

1868 *Hippurites polystylus* Pirona: 511.

MATERIAL. Three specimens from Qarn Mulayh, loose from lower part of sequence, BM LL41938–40, Skelton Collection; the species was also seen at Qarn Murrah (see Skelton *et al.* 1990: fig. 9a).

DESCRIPTION. Outer shell layer of medium thickness with numerous secondary pillars. Inner shell layer of right valve slightly thicker than outer shell layer, recrystallised.

COMMENTS. Swinburne *et al.* (1992) have shown that the supposed evolutionary sequence of *Pironaea* 'species' described as Maastrichtian in Serbia are more likely to be of Campanian to earliest Maastrichtian age.

Family **RADIOLITIDAE** d'Orbigny, 1847
(as Radiolidae, *emend.* Gray, 1848: 439)
Subfamily **RADIOLITINAE** d'Orbigny, 1847
Genus ***PRAERADIOLITES*** Douvillé, 1902, p. 467

TYPE SPECIES. *Radiolites fleuriaui* d'Orbigny, 1842, from the Cenomanian of Le Mans, by original designation.

DESCRIPTION. Ligamentary invagination of right valve usually present. Right valve elongate, left valve operculiform.

Praeradiolites* cf. *subtoucasi Toucas, 1907 Pl. 6, figs 3, 4

cf. 1907 *Praeradiolites subtoucasi* Toucas: 31, pl. 3 (13), figs 8, 9.

MATERIAL. Four specimens from Jebel Rawdah, section 4, from the Simsima Formation, bed 1, BM LL41941–44.

DESCRIPTION. A slightly distorted attached (right) valve, 'D'-shaped in transverse section, which has developed a secondary bilateral symmetry about a dorso-ventral plane. Moderately wide radial bands are separated by a narrower sinus, on the 'flat face' which is formed at the postero-ventral margin. The two radial bands are wider than the central sinus and all three are deep below the plane of commissure. Internally the symmetry differs from the outside, with the ligamentary invagination set at about 30 degrees to the posterior of the axis bisecting the external 'D' shape.

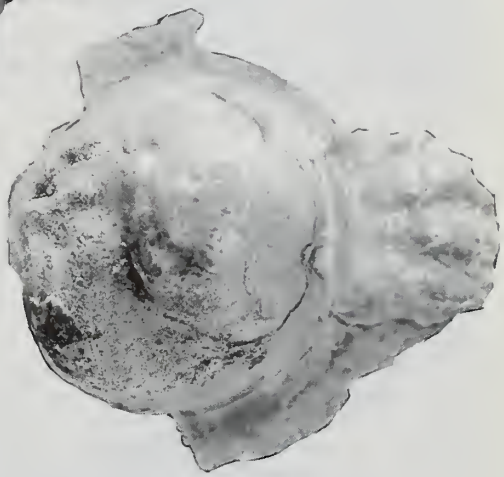
COMPARISON WITH OTHER SPECIES. The sinuses are deeper

PLATE 7

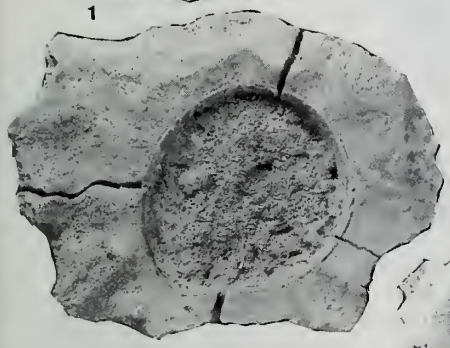
Figs 1–4 *Durania* cf. *gaensis* (Dacqué), Jebel bu Milh, section 1, Qahlah Formation; all × 0·75; **1**, BM LL41922, individual from first clump, natural section showing shell layers and tabulae of right valve and part of surface and myophore of left valve; **2**, BM LL41923, individual from second clump, commissural surface of right valve; **3**, BM LL41924, individual with domed left valve from third clump, internal mould with some shell adhering; **3a**, postero-dorsal view; **3b**, basal view of right valve; **3c**, anterior dorsal view; **4**, BM LL41922, second individual from first clump; **4a**, postero-dorsal view; **4b**, postero-ventral view.

1

3a



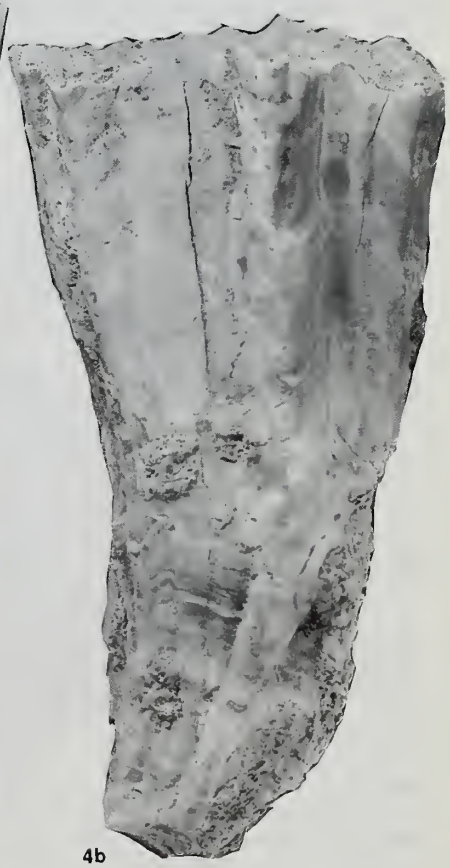
3b



2

3c

4a



4b

than those of *P. aristidis* (Munier-Chalmas, 1888) as figured by Toucas (1907, pl. 6 (16), figs 9, 10). They are more similar to *P. boucheroni* (Bayle) as figured by Toucas (1907, pl. 3 (13), fig. 10 only) and to *P. subtoucasi* Toucas (1907, pl. 3 (13), figs 8, 9).

Genus ***RADIOLITES*** Lamarck, 1801

DESCRIPTION. Widely biconical with upper valve shorter than lower right valve. Outer layer of fixed right valve thick with calcite cellular structure radially stretched. Arête cardinale usually present, usually short.

?Radiolites sp. Pl. 6, fig. 2

MATERIAL. Three specimens From Jebel Bu Milh, section 1, from the Qahlah/Simsima boundary, BM LL41945–46; Jebel Bu Milh, section 2, beds 7, 8, BM LL41947; one probable specimen from Jebel Rawdah, section 2, from scree, LL41980.

DESCRIPTION. The simple smooth radial bands, the flaring growth rugae-like stacked projecting cones, and the radially aligned cell pattern of the outer shell layer of the right valve are similar to *Radiolites*, particularly the groups of *Radiolites radiosus* and *R. sauvagesi* (Toucas 1908). The radial bands are not thrown into stong folds and therefore this species does not belong to *Praeradiolites*. No arête cardinale is visible and it may well be absent. This is a common trend in many rudist lineages and we suspect that it may happen independently in this form of *Radiolites*.

Subfamily **PSEUDOPOLYCONITINAE** Sladić-Trifunović, 1983b, p. 239
(*ex*. Pseudopolyconitidae Sladić-Trifunović1983b, emend. herein)
Genus ***PSEUDOPOLYCONITES*** Milovanović, 1937
[*Pseudopolyconites* Milovanović, 1935, was invalid because no type species was originally designated, in contravention of ICZN Rules, Art. 13A (b)]

TYPE SPECIES. *Pseudopolyconites parvus* Milovanović, 1935.

Pseudopolyconites* aff. *parvus Milovanović, 1935 Pl. 6, fig. 5

1934 *Pseudopolyconites parvus* Milovanović: 188, 252 (*nomen nudum*).
aff. 1935 *Pseudopolyconites parvus* Milovanović: 54–70, figs 1b–8.
aff. 1937 *Pseudopolyconites parvus* Milovanović; Milovanović: 4–14, figs 2–9.

MATERIAL. Two specimens from Qarn Murrah, BM LL41978–79, and one specimen collected loose at Qarn Mulayh, BM LL41974; all Skelton Collection.

REMARKS. The specimen LL41974 is well-preserved and shows the spines and a wide smooth ventral radial band. The arête cardinale is long and narrow, with a typically rounded to ovoid distal end. The left valve LL41978 shows the arête cardinale and the spine bases on its upper surface.

Subfamily **BIRADIOLITINAE** Douvillé, 1902
Genus ***BIRADIOLITES*** d'Orbigny, 1850

TYPE SPECIES. *Biradiolites canaliculatus* d'Orbigny, 1850 (ICZN Opinion pending).

Biradiolites aff. ***baylei*** Toucas, 1909 Pl. 8, figs 1, 2

aff. 1909 *Biradiolites baylei* Toucas: 119, pl. 24 (9), figs 9, 10.
1909 ?*Biradiolites royanus* (d'Orbigny); Toucas: 103, pl. 19 (4), figs 34–38.
cf. 1909 *Biradiolites aquitanicus* Toucas: 107, pl. 20 (5), fig. 20.
?1967 *Biradiolites bulgaricus* Pamouktchiev: 35, pl. 1, fig. 4; pl. 2, figs 3, 4.

MATERIAL. Five specimens from Jebel Huwayyah, section 2, four from the top of the *Loftusia*-Beds, BM LL41799–41802, one from the *Loftusia*-Beds, BM LL41815, Skelton Collection; one specimen from Jebel Bu Milh, loose, but probably from the basal gastropod bed of the Simsima Formation at Jebel Bu Milh, BM LL41805.

DESCRIPTION. Right valve with secondary approach to bilateral symmetry. Dorsal margin convex-alate, with a central (dorsal) raised portion, which is itself centrally grooved in a small specimen. Has strong 'lateral' carinae which curve downwards, giving the appearance of a stretched bow when the smooth dorsal surface is viewed. Ventral margin of right valve with wide radial bands separated by an acute carina that forms a prominent downward 'V' at about the same level as the 'lateral' carinae.

REMARKS. *B. baylei* was a lateral clinger, on its broadly expanded antero-dorsal face. The latter feature, and the anterior-ward leaning of the interband, suggest Toucas' group of *B. fissicostatus*, of which *B. baylei* is the Maastrichtian representative.

A specimen in the Trechmann collection, identified by Chubb (1971) as *Bournonia thiadensi* Vermunt from the Maastrichtian of Jamaica has similar plications on the ventral face of the lower valve, but a wider and flatter central area on the reverse side and in that way resembles the next species.

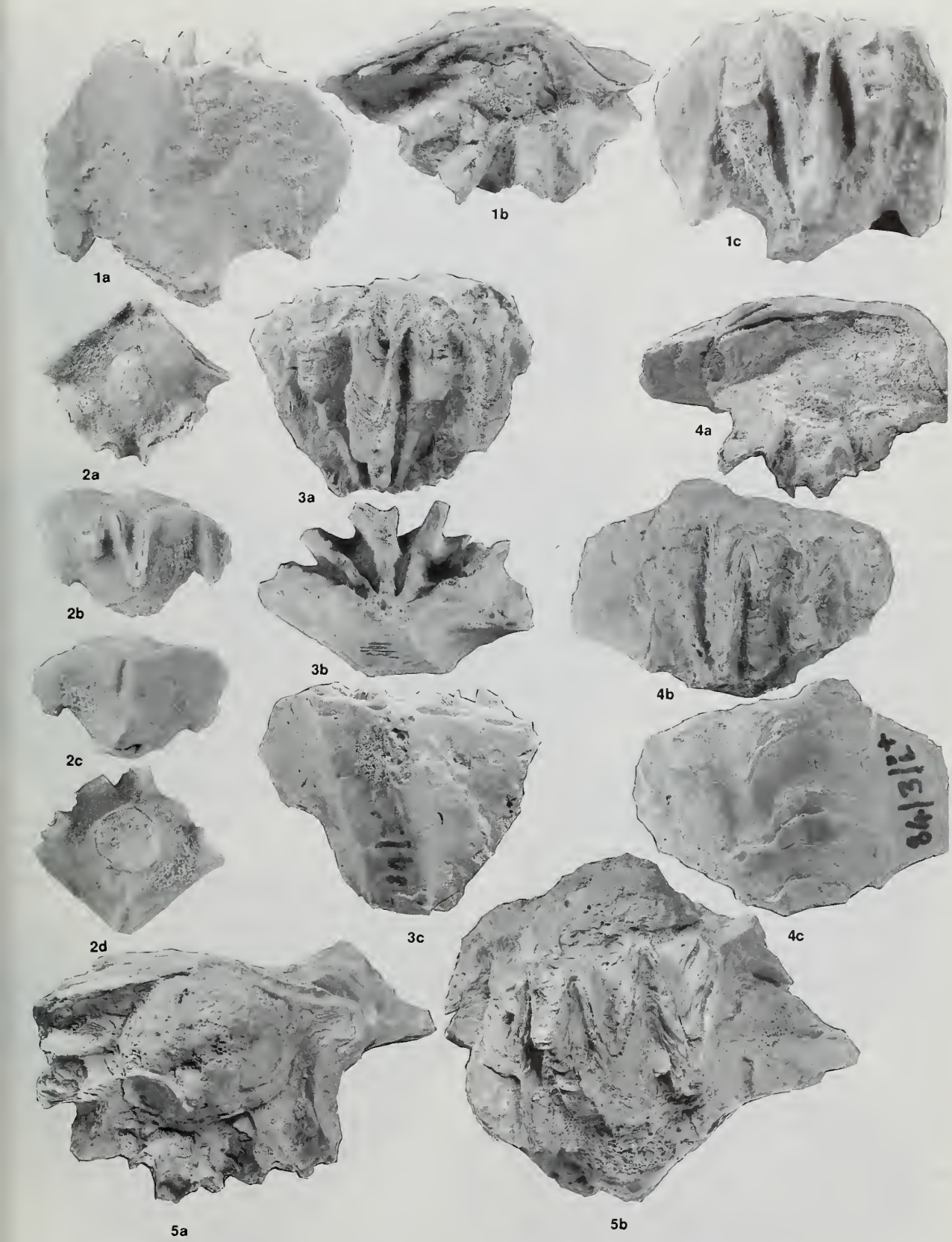
?Biradiolites aff. *baylei* Toucas, 1909 Pl. 8, figs 3–5

MATERIAL. Six specimens from the central eastern face of Jebel Faiyah, loose on lower part of the Simsima Formation, BM LL41793–98, Skelton Collection; one specimen from Jebel Rumaylah, from the lower *Dictyoptychus* level, LL41814, Skelton Collection; two specimens from Jebel

PLATE 8

Figs 1, 2 *Biradiolites* aff. *baylei* Toucas, Jebel Huwayyah, section 2, *Loftusia*-Beds, beds 3–8; × 1·5; **1**, BM LL41800; **1a**, dorsal view; **1b**, view of left valve; **1c**, ventral view; **2**, BM LL41799; **2a**, view of left valve; **2b**, ventral view; **2c**, dorsal view; **2d**, basal view of right valve.

Figs 3–5 *Biradiolites* ?aff. *baylei* Toucas, Jebel Faiyah centre, loose from lower part of Simsima Formation, Skelton Collection; × 0·75; **3**, BM LL41794, **3a**, ventral view; **3b**, basal view of right valve; **3c**, dorsal view; **4**, BM LL41796; **4a**, view of left valve; **4b**, ventral view; **4c**, dorsal view; **5**, BM LL41795; **5a**, view of left valve; **5b**, ventral view.


1a
1b
1c
2a
2b
2c
2d
3a
3b
3c
4a
4b
4c
5a
5b

Faiyah, section 1, in hard limestone, ?from the lower Simsima Formation, BM LL41803–04; two specimens from Jebel Buhays, section 3, lower Simsima Formation, BM LL41810–11; three specimens (two conjoined) from Jebel Aqabah, BM LL41812–13; one specimen from Jebel Rawdah, section 2, bed 13, BM LL41806; one specimen from the same section, bed 23, BM LL41807; two others from the same section, loose, BM LL41808–09; one specimen from Jebel Rawdah, BM LL41816, loose, Skelton Collection; one specimen from Jebel Ja'Alan, southern Oman Mountains, west side, lower Simsima Formation, BM LL41817, Skelton Collection.

COMMENTS. Similar to *Biradiolites* aff. *baylei* but with an additional carina between the dorsal radial band and the posterior carina. The radial bands are relatively narrower than in *B.* aff. *baylei*. A number of species of this complex have been described by Pamouktchiev (1967); Pons *et al.* (1992) in a study of specimens from Somalia suggested that the distinctions are unjustified.

Genus ***GLABROBOURNONIA*** Morris & Skelton gen. nov.

TYPE SPECIES. *Glabrobournonia arabica* Morris & Skelton sp. nov.

DIAGNOSIS. Small genus with a cornute lower valve and a very low, slightly convex upper valve. Right valve smooth except for fine growth lines and three major sinuses in the shell margin which leave sinusoidal traces, one at the ventral margin, one at the dorsal margin and one centrally on the posterior margin. Upper valve with reticulate sculpture of fine radiatig ribs and concentric growth laminae.

REMARKS. At present we are aware of only one species. *Glabrobournonia* differs from *Bournonia* in being devoid of ribbing on the right valve.

Glabrobournonia arabica Morris & Skelton sp. nov. Pl. 9, figs 1, 2

HOLOTYPE. BM LL41873 from Jebel Rawdah, section 1, the lower Simsima Formation, bed 2, just below low Upper Maastrichtian ammonites and inoceramids.

PARATYPES. Jebel Rawdah, section 1, bed 2, LL41870–72; bed 3 and top bed 2, LL41874–95; loose, LL41869; section 4, bed 2, the basal rudist bed, LL41896–41916; Jebel Rawdah, southern flank, scree from Lower Simsima Formation, LL41818–22, Skelton Collection; Jebel Faiyah, section 2, lower Simsima Formation, LL41855–57; Jebel Thanais, lower Simsima Formation, LL41854; Jebel Buhays, section 1, LL41836–51, LL41917–21; LL41825–27, Skelton Collection; section 1, lower Simsima Formation, beds 4–10, LL41832–35; section 1b, loose, BM LL41852–53.

OTHER MATERIAL. Qarn Murrah, 50–60 m from bottom of section, LL41828 (16 specimens), LL41829–31, Skelton Collection; Jebel Huwayyah, section 1, beds 10–11, *Loftusia*-Beds, LL41858; section 2, beds 2–7, *Loftusia*-Beds, LL41859–68; LL41823–24, Skelton Collection.

DIAGNOSIS. As for genus.

DESCRIPTION. Mostly smooth horn-shaped lower valve with two bands representing a downward sinuosity where the cellular structure is exposed; one band is anterior, the other is ventral, and there is a further posterior sinuosity where growth increments are more obvious than the cellular structure. Upper valve has exposed cellular structure radiating from excentric umbo, otherwise smooth, gently convex with a sinuous margin to fit lower valve.

Subfamily **SAUVAGESIINAE** Douvillé, 1908
Genus ***DURANIA*** Douvillé, 1908

TYPE SPECIES. *Hippurites cornupastoris* Des Moulins, 1826, from the Turonian of France.

REMARKS. The specimens of *Durania* from the Qahlah Formation of Jebel Bu Milh are well-preserved, but even this material does not give us sufficient information concerning ecophenotypic variation. Different 'morphs' from different horizons are listed separately but we do not know whether they are different species.

Durania* cf. *gaensis (Dacqué, 1903) Pl. 7, figs 1–4

cf. 1903 *Radiolites ga'ensis* Dacqué: 374, pl. 35, figs 7–9.
cf. 1909 *Sauvagesia gaensis* (Dacqué); Toucas: 85, pl. 16 (17), figs 3–5.
?1909 *Sauvagesia flicki* Toucas: 84, 85, pl. 16 (17), figs 6–8.
cf. 1910 *Durania gaensis* (Dacqué); Douvillé: 50.

LOCALITIES OF PREVIOUSLY FIGURED MATERIAL. Dacqué's type material came from Ga'a near Abu Roash, Egypt, and was said by Douvillé (1910) to be Turonian in age; Toucas' material occurs with *Lapeirousia* and was said to occur from Coniacian to Maastrichtian in Tunisia.

MATERIAL. Three clumps from Jebel Bu Milh, section 1, from the upper part of the Qahlah Formation, LL41922–24; two further doubtful clumps from Jebel Faiyah, one loose from section 1, the second from section 1b, bed 2b, BM LL41925–26.

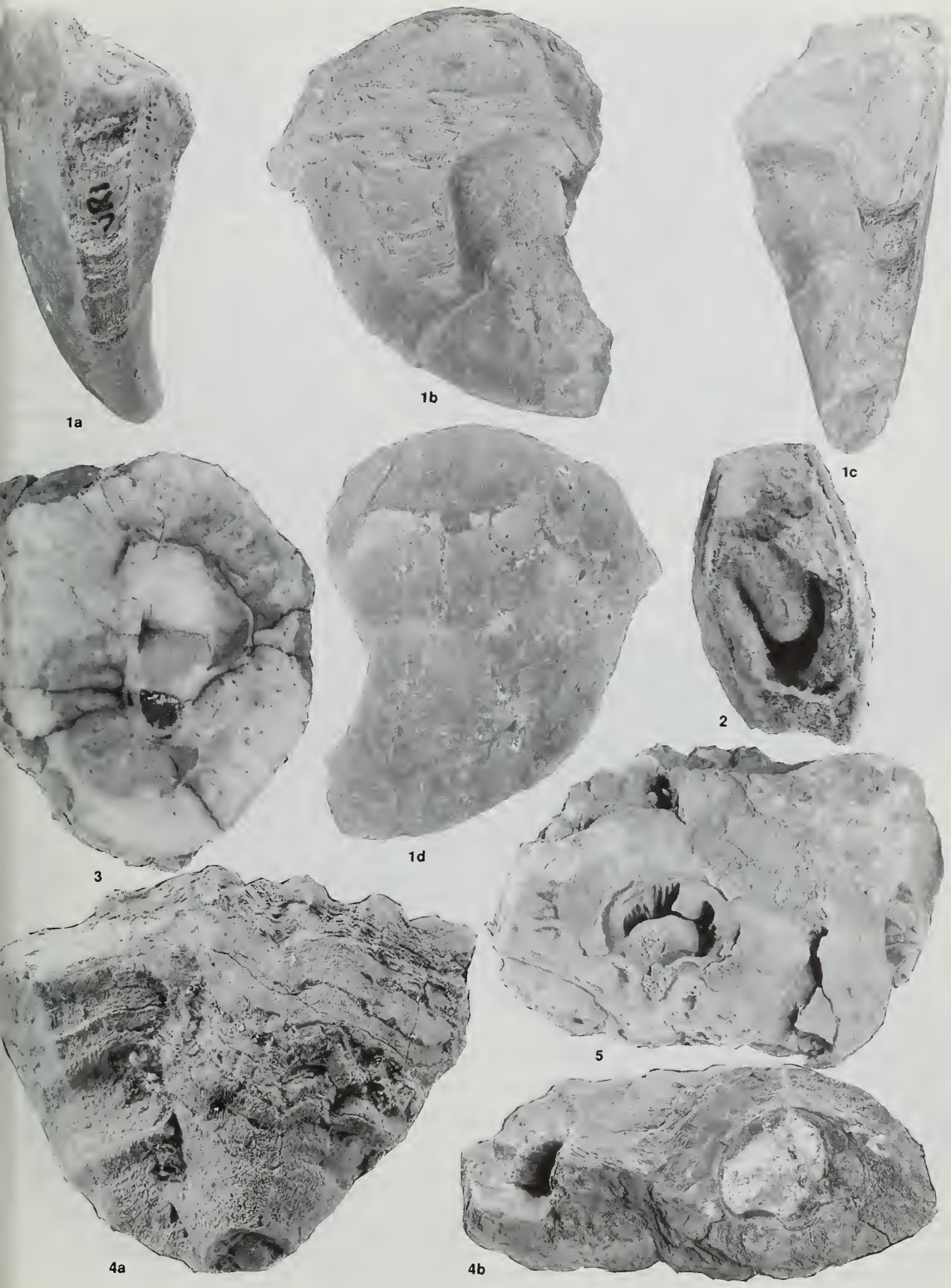
DESCRIPTION. Rather large, outer shell layer of right valve

PLATE 9

Figs 1, 2 *Glabrobournonia arabica* Morris and Skelton gen. nov., sp. nov.; **1**, Jebel Rawdah, section 2, Simsima Formation, bed 2, BM LL41873, holotype; **1a**, ventral view; **1b**, posterior view; **1c**, dorsal view; **1d**, anterior view; × 1·5; **2**, south end of Jebel Buhays, lower part of Simsima Formation, BM LL41825, paratype, Skelton Collection; view of internal mould of left valve; × 1·5.

Fig. 3 *Osculigera* cf. *vautrinioides* Vogel, probably from Qarn Murrah, BM LL22460, Iraq Petroleum Company Collection; polished section of right valve; × 1.

Figs 4, 5 *Lapeirousia* sp.; **4**, Jebel bu Milh, section 2, Qahlah Formation, bed 5, the acteonellid gravels; BM LL41955, conjoined pair of right valves; **4a**, ventral view; **4b**, view of commissural surface; × 1; **5**, Jebel Thanais, section 4, loose from lower part of Simsima Formation; BM LL41956, conjoined pair of individuals; view showing commissural surface with pseudo-pillars below internal mould of left valve; × 1.


1a
1b
1c
1d
2
3
4a
4b
5

with thin-walled polygonal cells resembling those of *Durania* rather than *Biradiolites*. LL41922 includes three specimens with the upper valve in place, which is slightly concave and smooth in the centre but develops low rounded plicae towards the margins. LL41924 includes one specimen with the upper, left valve present but, in this case it is hemispherically domed above the body-cavity of the right valve. We consider this to be a phenotypic variation, possibly related to the angle of the growth surface to the long axis of the right valve. Right valve steeply conical, 'D'-shaped in section, with wide and smooth, somewhat indented radial bands on the straight part of the 'D'. Radial bands separated by a large plication with two sub-plications at its crest. Rounded part of 'D' with approximately fourteen evenly distributed plicate ribs. Growing surface undulates with the plication of the outer shell sculpture.

Durania cf. *apula* (Parona, 1900) Pl. 6, fig. 6

1900 *Biradiolites apulus* Parona: 21, pl. 3, figs 1–3.Q:
1909 *Sauvagesia apulus* Parona; Toucas: 97, fig. 65.

MATERIAL. From Jebel Rawdah, section 2, bed 10, BM LL41951.

DESCRIPTION. Medium sized species with approximately 40 narrow vertical ribs on lower valve. Wide growth surface of outer shell layer of right valve, which is not plicated. Ventral radial band relatively narrow and somewhat concave, with fine radial striations. Dorsal radial band narrow with fine riblets. Radial bands separated by a convex interband with a few sub-plicae. Growth surface of right valve has single narrow round holes approximately 2mm in diameter at the mid-point of its width near the position of the radial bands. Similar features have been found in Santonian hippuritids and are being described by Skelton & Vicens (in prep.), who regard them as the crypts of parasitic or commensal organisms.

Durania form A Pl. 6, fig. 1

MATERIAL. From Jebel Huwayyah, section 1, Qahlah gravel, BM LL41948; two specimens from Qarn Mulayh, BM LL41949–50, Skelton Collection.

DESCRIPTION. Large form with approximately 70 ribs on the external surface of the right valve matched by undulations on the wide growth surface, and prominent down-twisted concave smooth dorsal radial band.

Durania form B Fig. 6

MATERIAL. From Jebel Rawdah, section 1, bed 4, BM LL41952; section 2, bed 6, BM LL41953; three specimens, section 2, loose, BM LL41954.

DESCRIPTION. Small species with approximately 40 evenly spaced bifurcating ribs. Outer shell layer of right valve relatively thin with a folded growth surface, each upward fold in the position of the interspace between the ribs.

REMARKS. The outer shell surface of the right valve and the growth form are similar to *Durania cornupastoris* as figured by Cobban, Skelton & Kennedy (1991: pls 1–3).

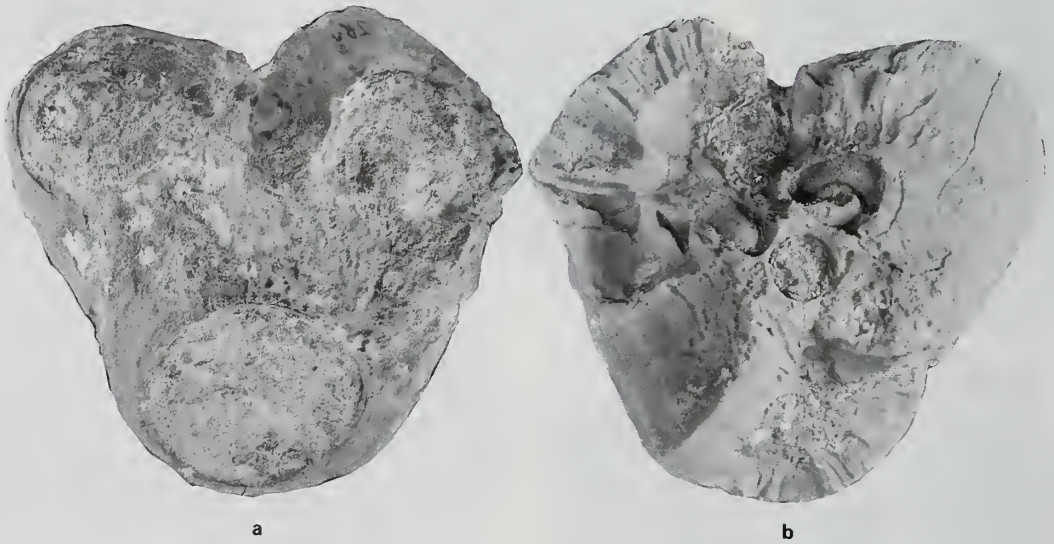


Fig. 6 *Durania* form B; a group of three conjoined individuals with the remains of a fourth on the under surface; BM LL41954, × 0·75.

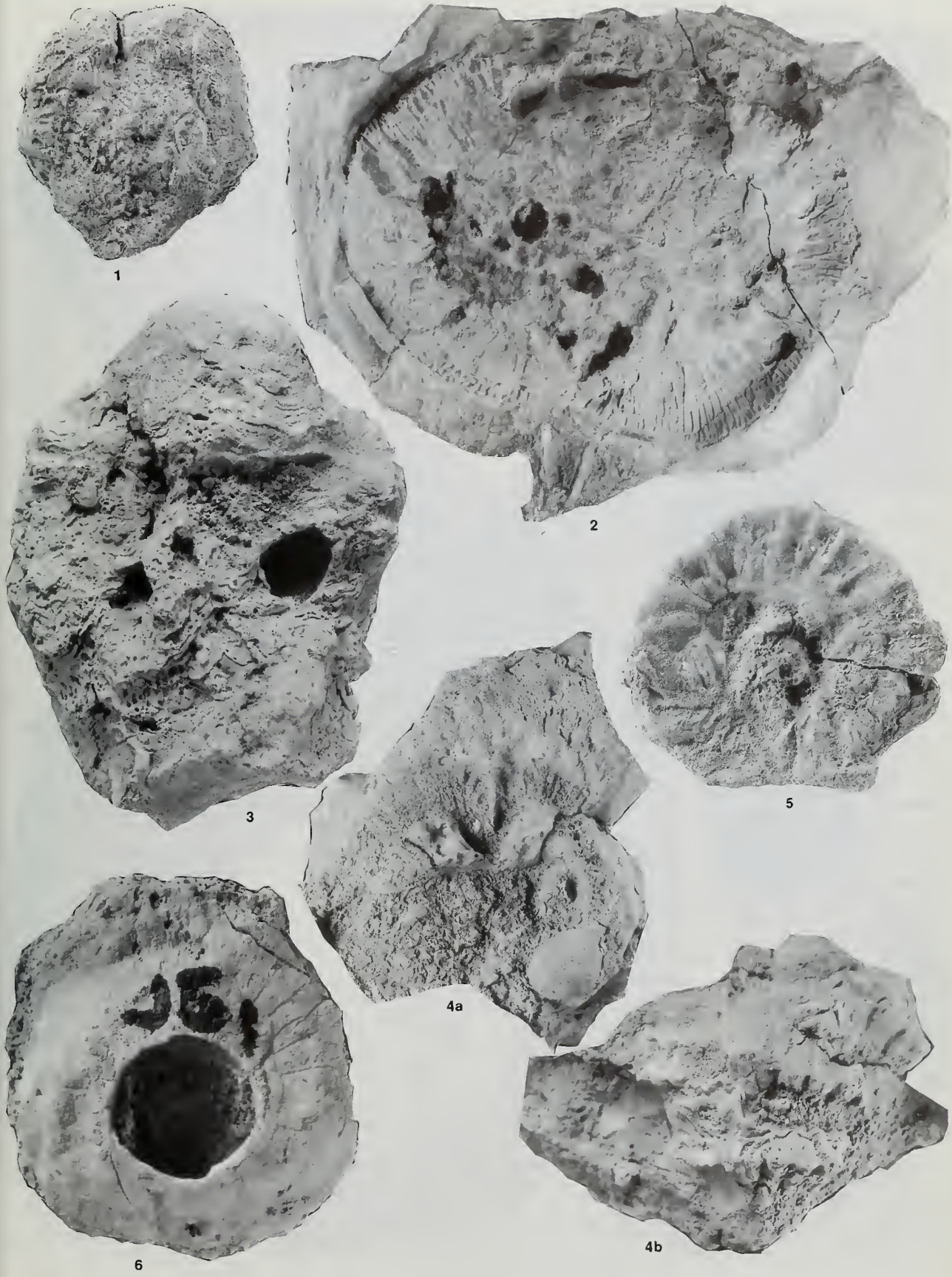
PLATE 10

Fig. 1 *Pseudosabinia* aff. *klinghardti* (Boehm), Jebel bu Milh, section 2, bed 7–8, ? uppermost bed of Qahlah sands; BM LL41964, view of commissural surface of right valve; × 1.

Figs 2–4 *Colveraia* aff. *variabilis* Klinghardt; **2**, Qarn Mulayh, LL41958, Skelton Collection, view looking down on rim of right valve showing the internal structure of the left valve; × 1; **3**, Jebel Thanais, loose from basal beds of Simsima Formation, BM LL41961, dorsal view of the two valves, × 1; **4**, central Jebel Faiyah, loose from lower part of Simsima Formation, BM LL41960, Skelton Collection; **4a**, view looking down on internal structure of left valve; **4b**, ventral view of right valve; × 1.

Fig. 5 *Osculigera* cf. *vauriniodes* Vogel, Qarn Murrah, BM LL41770, eroded section of right valve; × 1.

Fig. 6 *Lapeirousia* sp., Jebel Buhays, loose from basal beds of Simsima Formation, BM LL41957; minute pseudo-pillars just visible; in the lower part of the figure the emplacement of the last shell layer is divided below the pseudopillars; × 2.


1
2
3
4a
4b
5
6

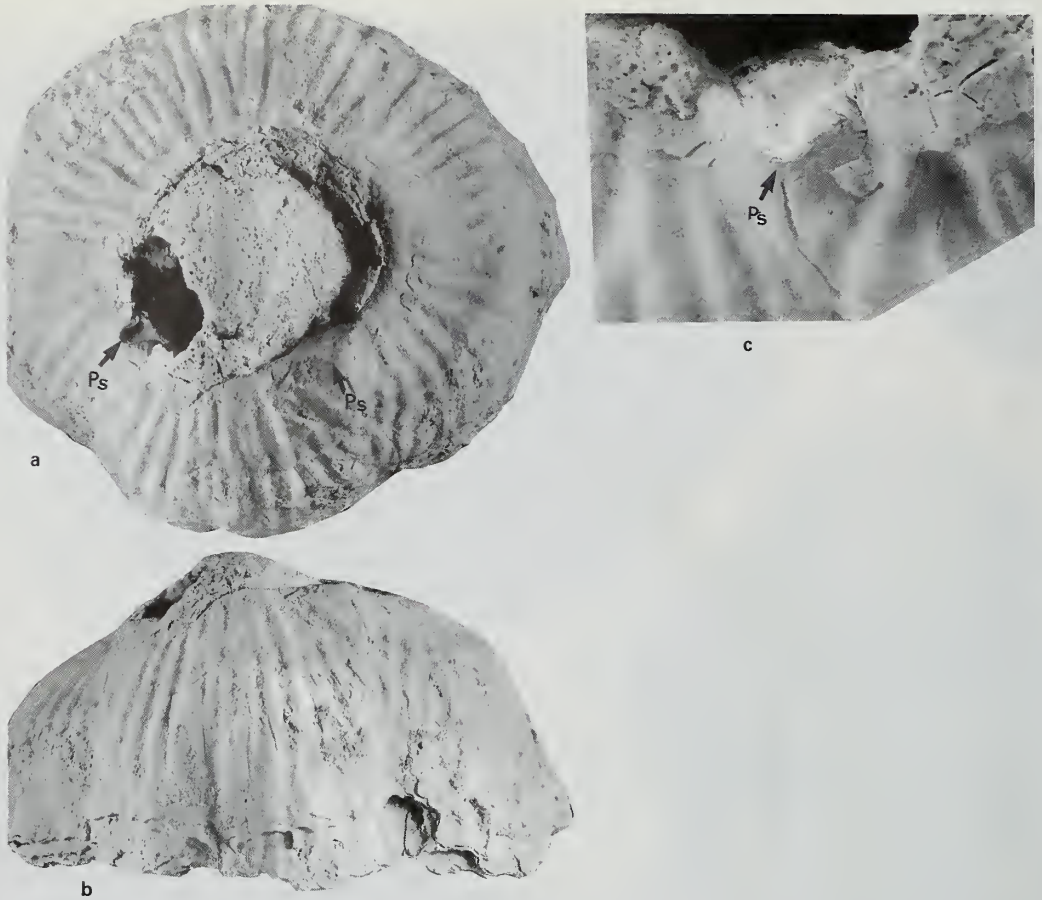


Fig. 7 *Lapeirousia jouanneti* Des Moulins, from the Upper Campanian, near Cognac, France, BM LL41976; **a, b**, upper and ventral view of a flat-based individual with pseudopillars marked, × 0·4; **c**, close-up of ventral pseudopillar showing its spout-like shape and division of the last layer of outer shell around it, × 1·5.

Durania spp.

Fragmentary or poorly preserved specimens that we can attribute to the genus *Durania* occur at most levels in the Qahlah and Simsima Formations: at Jebel Huwayyah, section 1, from bed 13, the basal Simsima conglomerate, the top rudist bed (two silicified specimens), and from near the top of the Simsima Formation approximately 6 m above the top oyster bed; at Jebel Rawdah, section 1, bed 2, and section 2, bed 16; and at Qarn Mulayh, a large thick-celled form with strangely shaped cells.

Subfamily **LAPEIROUSIINAE** Kühn, 1932
Genus ***LAPEIROUSIA*** Bayle, 1878

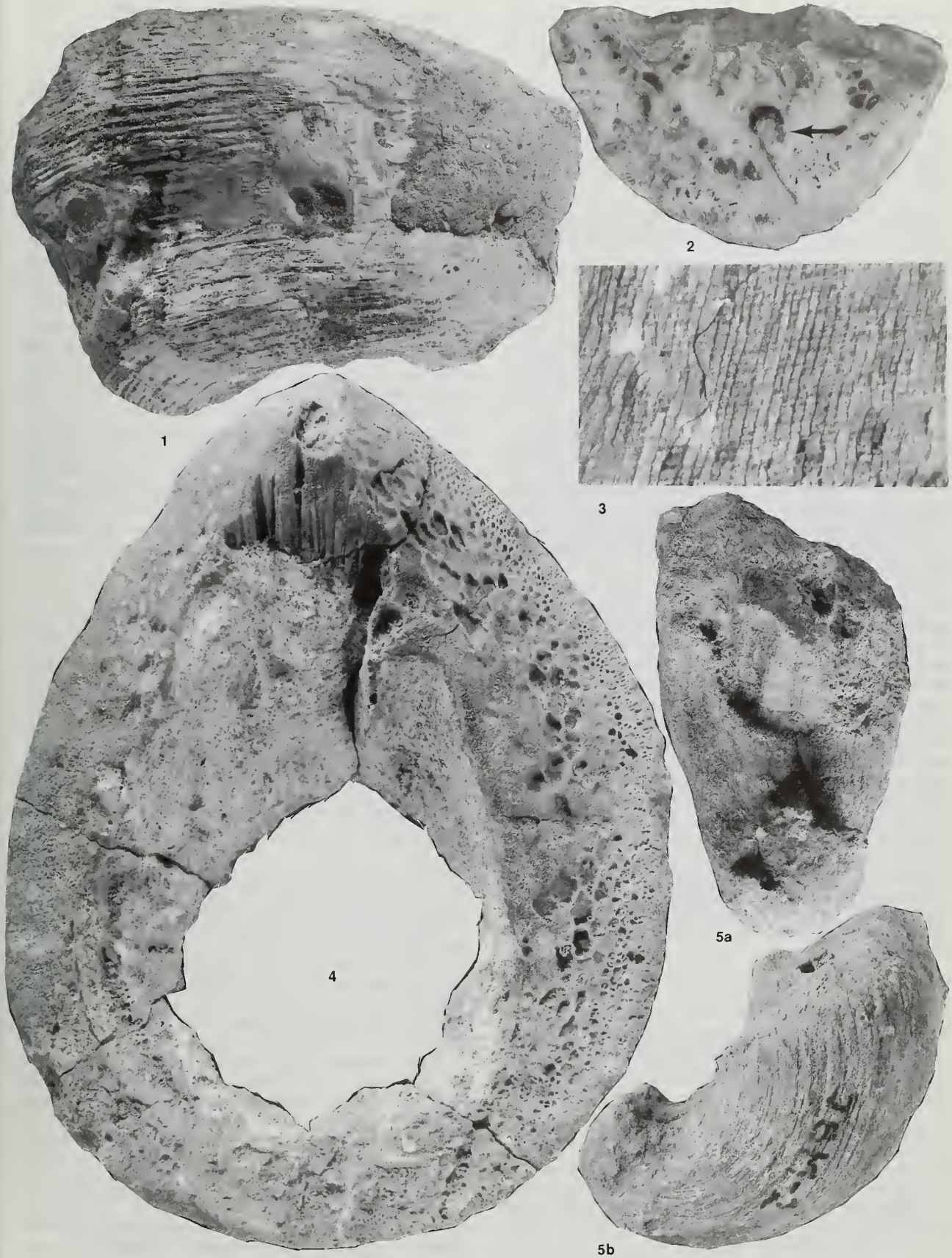
TYPE SPECIES. *Sphaerulites jouanneti* Des Moulins, 1826, Upper Campanian or Lower Maastrichtian, Aquitaine, France.

Lapeirousia sp. Pl. 9, figs 4, 5; Pl. 10, fig. 6

MATERIAL. Two small joined specimens from Jebel Bu Milh, section 2, from the acteonellid bed towards the top of the Qahlah Formation, BM LL41955; three specimens, two of which are joined, from Jebel Thanais, from scree below basal part of the Simsima Formation, BM LL41956; one from Jebel Buhays, section 1, LL41957.

PLATE 11

Fig 1–5 *Pseudosabinia* aff. *klinghardti* (Boehm); **1**, Jebel Fayah, basal *Durania*-facies of the Simsima Formation, BM LL41971, Skelton Collection; eroded valve showing striate appearance of the outer part of the inner shell layer; × 0·4; **2**, Virovi (between Lanac and Vestari, near Rtanj mine), eastern Serbia; BM LL41652, paratype of *Sabinia rtanjica* Pejović; section through right valvewith arête cardinale and ligament (arrowed); × 1·5; **3**, Qarn Murrah, BM LL41972, Skelton Collection; close up of cellular structure of outer shell layer of right valve; × 5; **4, 5**, Jebel bu Milh, section 2, Qahlah Formation; **4**, BM LL41963, eroded commisural surface of a right valve; × 1; **5**, BM LL41962, an eroded left valve; **5a**, oblique dorsal view; **5b**, posterior view; × 0·6.


1
2
3
4
5a
5b

DESCRIPTION. Small ovoid conical species, with the right valve approximately 75mm high and its marginal surface an ovoid approximately 37x45 mm. The structure of the pseudopillars of *Lapeirousia jouanneti* is shown in Fig. 7.

Genus *OSCULIGERA* Kühn, 1932

TYPE SPECIES. *Osculigera cleggi* Kühn, 1932, by original designation.

SYNONYM. ?=*Vautrinia* Milovanović 1938 (type species, *Lapeirousia syriaca* Vautrin, 1933, by original designation).

REMARKS. Species differ in degree of complication of undulation of growth surface of outer shell layer.

Osculigera* cf. *vautrinioides Vogel, 1970 Pl. 9, fig. 3; Pl. 10, fig. 5

cf. 1970 *Osculigera vautrinioides* Vogel: 69, pl. 7, figs 3, 4, 6; pl. 8, fig. 3.

MATERIAL. 21 fragmentary specimens from Qarn Murrah, BM LL41770–80; BM LL41781–90, Skelton Collection; also from the same locality BM LL41791 (a block with six conjoined juveniles), and BM LL41792 (one specimen and some fragments), Skelton Collection; also BM LL22460–63 (identified by A. Grubić as *O. magna* Kühn) labelled Trucial Coast, but almost certainly the same locality, Iraq Petroleum Co. Collection (RN 39/2,4,5.).

DESCRIPTION. Right valve varies from a low inverse cone to a subcylinder. Surface with fine, low, even vertical ribs. Pseudopillars project into body-cavity in low but obvious gentle curves. Outer shell layer of right valve very thick, about equal to the diameter of the body-cavity. Shell margin approximately planar. Cells sub-polygonal and rather short, inner shell layer very thin. Approximately 24 radiating undulations, each topped by a row of radially elongate, radiating projections (secondary pseudopillars of Kühn) on the secreted marginal surface, which occasionally branch as they approach the outer shell surface. Up to about 12 projections, regularly spaced within each line, which are not visible in very small individuals.

COMMENT. It is very difficult to see consistent differences between the species described by Kühn and Vogel. The shell thickness and form of the radiating tuberculate undulations seem to be very similar to the specimen figured by Vogel as *O. vautrinioides*.

Subfamily **JOUFIINAE** Karacabey-Öztemür 1981

GENERA INCLUDED. *Colveraia* (?=*Dechaseauxia*) and others from Serbia and Romania, *Joufia*, *Pseudosabinia* gen. nov. and an undescribed genus for *Radiolites albonensis* Toucas, 1908.

REMARKS. These are highly specialised radiolitids with pallial canals and well-developed arête cardinale. They differ from the the subfamily Chiapasellinae Alencaster, which lack the ligamentary invagination. The arête cardinale of one species of the family, *Pseudosabinia rtanjica*, has the split inner ligament preserved on its inner surface (Pl. 11, fig. 2). They are fixed by the right valve.

Genus *COLVERAIA* Klinghardt, 1921

TYPE SPECIES. *Colveraia variabilis* Klinghardt, 1921, by original designation.

SYNONYMS. *Branislavia* Sladić-Trifunović, 1983a; ?*Dechaseauxia* Tavani, 1949.

Colveraia* aff. *variabilis Klinghardt, 1921 Pl. 10, figs 2–4

MATERIAL. One specimen from Qarn Mulayh, BM LL41958; one specimen from Qarn Murrah, BM LL41959; one specimen from Jebel Faiyah, north-west face, low in the Simsima Formation, low in the *Dictyoptychus*-facies, BM LL41960, all Skelton Collection; one specimen from Jebel Thanais, loose from basal Simsima Formation, BM LL41961.

DESCRIPTION. Moderately thick calcitic outer shell layer of the right valve with a narrow elongate arête cardinale. Canals obvious in the inner shell layer of both valves. In the right valve a single row of large, subquadrate canals separate the sockets and myophores from the outer shell layer. In the left valve the canals are somewhat narrower and radially elongate and penetrate the teeth and myophores. In one specimen (Pl. 10, fig. 4a) the outer surfaces of both the teeth and the myophores are longitudinally ridged, with the ridges apparently formed by the canal walls, which interdigitate with ridges on the muscle attachment surface of the opposing valve.

Genus *PSEUDOSABINIA* Morris & Skelton gen. nov.

TYPE SPECIES. *Pseudosabinia klinghardti* (Boehm, 1927).

INCLUDED SPECIES. *Sabinia klinghardti* Boehm, 1927, *Sabinia serbica* Kühn & Pejović, 1959, and ?*Sabinia rtanjica* Pejović, 1967.

DIAGNOSIS. Both valves extended, conical, gently curved. Outer shell layer finely cellulo-prismatic to compact in the right valve, thinner and smooth in the left valve. Well-developed arête cardinale projecting between two close, well-developed teeth, flanked by radiolitiform myophores in left valve. Inner shell canaliculate throughout in both valves.

REMARKS. Originally assigned to *Sabinia*, the species of this genus are recognized by the finely polygonal cellulo-prismatic structure of the outer calcitic layer of the right valve, and for their radiolitiform myocardinal apparatus. In *P. serbica* the cells appear to be present in some areas of the right valve outer layer (Kühn & Pejović , 1959: figs 7, 8), whereas they occur throughout the outer shell layer of the right valve of *S. klinghardti*. The thickness and surface sculpture of coarse, zig-zag growth rugae of this outer shell layer are similar in *S. serbica* and *S. klinghardti*.

In the interpretation of Philip (1986) all species of *Sabinia* are considered to be related and are off-shoots of the Radiolitidae that have secondarily reduced the outer calcitic shell layer of the right valve. We consider that there may be at least two distinct genera within the genus *Sabinia* as presently constituted, and that these may be quite unrelated. The features of the true *Sabinia* with its type species, *Sabinia anienis* Parona 1908, may relate it to the Plagioptychidae.

NOTE ON THE TYPE SPECIES OF *SABINIA*. Parona described three species: in sequence they were *S. sublacensis*, *S. sinuata*

and *S. anienis* from the Pietra di Subiaco, Late Cretaceous, of Monte Affilano, Valle dell'Aniene, Provincia di Roma (the type specimens are in Rome). All three nominal species may be merely varieties. In Parona's material a septum cuts off the posterior accessory cavity from the body-cavity in the left valve (Parona, 1908: figs a, c). It runs between the anterior tooth and the postero-ventral margin, and could be equivalent to the septum in the left valve of the plagioptychids. Parona does not describe the structure of the outer shell layer of the right valve in any detail.

Pseudosabinia aff. ***klinghardti*** (Boehm, 1927) Pl. 10, fig. 1; Pl. 11, figs 1–5

aff. 1927 *Sabinia klinghardti* Boehm: 205, pl. 15, figs 1, 2; pl. 16, fig. 1.
?aff. 1927 *Schiosia bilinguis* Boehm: 207, pl. 18, figs 1a–1c.
aff. 1967 *Pseudosabinia rtanjica* Pejovič : 295–97, pl. 1, fig. 1.
aff. 1986 *Sabinia rtanjica tunisiensis* Philip: 248, 49, pl. 1, figs 1–6.

TYPES. The holotype, BM L49455 from the Campanian-Maastrichtian, east of Hereke and west of Tauchanly, Bythinia, north-west Turkey, has both valves preserved; the paratype, BM L49454 from the same locality, is a much larger specimen of a crushed right valve. The holotype of *Schiosia bilinguis*, BM L50929, is from the 'Upper Senonian' between Herake and Tauchanly, Bithynia. BM LL41652 is an unfigured paratype of *P. rtanjica* Pejović, from near Rtanj mine, eastern Serbia.

NEW MATERIAL. From Qarn Murrah, a large crushed right valve with most of the outer shell layer missing except for a thin layer remaining, together with a second crushed valve which may be left or right, BM LL41972, Skelton Collection; four specimens from Jebel Bu Milh, section 2, Qahlah Sands, BM LL41962–65; two possible specimens from Jebel Rawdah, section 4, bed 1, the basal rudist bed, BM LL41966–67, and another small left valve that shows well-developed pallial canals and a narrow arête cardinale, BM LL41968; a large left valve from the north-west face of Jebel Faiyah, Simsima Formation, the *Durania*-facies, BM LL41971, and a small left valve from central Jebel Faiyah, BM LL41981, both Skelton Collection.

DESCRIPTION. The material from Qarn Murrah is badly crushed but does show the cellular outer shell layer (Pl. 11, fig. 3). The large, horn-like right valve (Pl. 11, fig. 4), at least 16 cm long, has a long narrow arête cardinale, a thick inner shell consisting of irregularly polygonal pallial canals, fine at the valve margin, becoming coarser inwards, and prominent cystose tabulae. Accessory cavities are apparently absent. There are two sockets for prominent prong-like teeth with longitudinal grooves and ridges either side of a low, ridge-like tooth, immediately ventral to the arête cardinale. The myocardinal arrangement is not capriniform. The small right valve of Pl. 10, fig. 1 shows the arête cardinale straddled by the ridged sockets for the teeth. Two equally prominent teeth are present in the fixed left valve of Pl. 11, fig, 5.

REMARKS. The progression from small to larger pallial canals in the left valve of *S. bilinguis* Boehm is similar to the pattern in the present species, otherwise Boehm's species has very few characters preserved. The outer shell layer of the right valve of *Pseudosabina rjtanjica* is thin (less than 1 mm, *fide* Philip) and of dense fibrous calcite, ie not cellular as in *P. klinghardti*. This seems to be the only difference, but is confirmed by our material. Pejović (1967) and Philip (1986) suggest that a row of canals separating the myophores from the body-cavity distinguishes *P. rtanjica* from *P. klinghardti*. Careful inspection of Boehm's holotype leads us to the conclusion that this difference does not exist. The myophores actually have a purely radiolitiform arrangement, albeit with contained canals, and face outwards opposing the inner surface of the right valve.

Pejović's (1967) description of *Sabinia rtanjica* was based only on eight specimens of the upper, left valve, in which the myophores were stated to be separated from the living chamber by a number of pseudocanals, characterized by regularly spaced tabulae and not considered homologous with the canals of the Caprinidae. A well- preserved small left valve collected by one of us (PWS) from the ?Lower Campanian of Monte Kamilja, near Leposavić in south-west Serbia, confirms the description of *P. rtanjica* in having large canals on inner sides of the myophores. However, this feature is in fact the coarse canaliculate structure of the myophoric apophyses and is also present in the holotype of *Pseudosabinia klinghardti*. Philip's (1986) Tunisian form differs from Pejović's original description in the length of the arête cardinale which reaches well between the teeth, unlike that in the Serbian original which, it is claimed, only reaches the top of the teeth/sockets. Inspection of Pejovič 's 1967, pl. 1, fig. 1 suggests that this is incorrect. Secondly Philip stated that the pallial canals of the lower (right) valve are of oval section in the Tunisian form, but oval and polygonal in the nominal subspecies. He also claimed that the upper valve canals have a suboval section in the Tunisian form, but these are pentagonal, hexagonal or triangular in the nominal subspecies. We suspect that these latter two distinctions reflect only the diagenetic growth of fibrous cement crust within the canals of the Tunisian material.

Pseudosabinia rtanjica has a very thin, compact outer shell layer in the right valve, according to Philip (1986), which is in contrast to the much thicker outer shell layer of *Pseudosabinia klinghardti*, although there are dense areas in the outer part of this layer in Boehm's holotype. This seems to be supported by our rather poorly preserved material, although a specimen with part of both valves preserved, apparently of *P. rtanjica*, from Serbia, kindly donated from Mdm. Pejović, shows a thin zone of cells on the innermost zone of the outer shell layer grading into dense structure in the outer part. This suggests the possibility of intergradation between the two taxa. Inspection of further material would be required to confirm this.

ACKNOWLEDGEMENTS. We would like to thank Diana Clements for considerable help in both sorting the material and preparing the manuscript. We are indebted to Phil Crabb for taking the photographs, and to Tony Wighton and his colleagues for cutting the sections of the rudists.

REFERENCES

Boehm, J. 1927. Beitrag zur Kenntniss der Senonfauna der bithynischen Halbinsel. Palaeontographica **69**: 187–222, pls 11–18.

Chubb, L. J. 1971. Rudists of Jamaica. *Palaeontographica Americana*, **7** (45): 161–257, pls 27–58.

Cobban, W. A., Skelton, P. W. & Kennedy, W. J. 1991. Occurrence of the rudistid *Durania cornupastoris* (Des Moulins, 1826) in the Upper Cretaceous Greenhorn Limestone in Colorado. *Bulletin of the United States Geological Survey, Shorter Contributions to Paleontology and Stratigraphy, 1985 (D): D1–D8, 3 pls.*

Cox, L. R. 1933. The evolutionary history of the rudists. *Proceedings of the Geologists Association*, **44**: 379–88.

Dacqué, E. 1903. Mittheilungen uber den Kreidecomplex von Abu Roash bei Cairo. *Palaeontographica*, **30** (2) (4): 337–92, pls 34–36.

Defrance, J. L. M. 1821. *Dictionaires des sciences naturelles*, **18–22**. Paris.

Des Moulins, C. 1826. Essais sur les sphérulites qui existent dans les collections de MM. F. Jouannet et C. Des Moulins, et considerations sur la famille à laquelle ces fossiles appartiennent. *Bulletin de l'Histoire Naturelle Société Linnéenne de Bourdeaux*, **5** (1): 141–43.

Douvillé, H. 1888. Etudes sur les Caprines. *Bulletin de la Société géologique de France* (3) **6**, 699–730, pls. 22–25.

—— 1890–94. Études sur les rudistes. Révision des principales espèces d'Hippurites. *Mémoire no. 6; Mémoires de la Société Géologique de France; Paléontologie*, **1** (1890): 1–32, pls 1–3 (15–17); **2** (4) (1892): 33–56, pls 4–7 (18–21); **3** (4) (1893): 57–94, pls 8–15 (19–26); **4** (2) (1894): 95–138, pls 16–20 (6–10).

—— 1895–97. Études sur les rudistes. Distribution régionale des Hippurites. *Mémoire no. 6; Mémoires de la Société Géologique de France; Paléontologie*, **5** (1895): 139–188, pls 21–28 (8–15); **7** (3) (1897): 189–236, pls 29–34 (13–18).

—— 1902. Classification des radiolites. *Bulletin de la Société Géologique de France*, (serie 4) **11**: 461–482, pl. 15, figs 1–8.

—— 1904. Études Géologiques ; part 4, Paléontologie. Mollusques fossiles *in:* de Morgan, J. *Mission Scientifique en Perse*, **3**: 189–380, pls 25–50. Leroux, Paris.

—— 1905. Observations, *in* J. de Morgan. Note sur la géologie de la Perse et sur les travaux paléontologiques de H. Douvillé sur cette region. *Bulletin de la Société géologique de France*, (4) **5**: 170–189.

—— 1910. Études sur les rudistes. Rudistes de Sicile, D'Algérie, d'Égypte, du Liban et de la Perse. *Mémoires de la Société Géologique de France*, **41**: 1–84, pls 1–7.

—— 1927. Nouveaux rudistes du Crétacé de Cuba. *Bulletin de la Société Géologique de France*, (4) **27**: 49–56, pl. 4.

Gili, E. & Skelton, P. W. 1994. Classificació paleoecològica de les formes dels rudistes – una eina per a l'anàlisi paleoambiental. *Butlletí de la Instució Catalana d'Història Natural*, **61** (Sistemes I Processos): 97–116.

Gray, J. E. 1848. On the arrangement of the Brachiopoda. *Annals and Magazine of Natural History*, (2) **2** (12): 435–40.

Grubić, A. 1980. *Torreites milovanovici* sp. nov. iz Omana. *T. coxi* sp. nov it *T. chubbi* sp. nov sa Jamajke, nov prikaz roda *Torreites* Palmer i osvrt na znacaj njegovog paleogeografskog rasprostranjenja. *Vestnik zavod za geoloska i geofizicka Istrazivanja*, A **37**: 81–99, pls 1, 2.

Karacabey-Öztemür, N. 1981. Three new species of the genus *Miseia* and proposal of a new subfamily of Radiolitidae. *Bulletin of the Mineral Research and Exploration Institute of Turkey*, **92**: 40–46, pls 1–2.

Klinghardt, F. 1921. Die Rudisten. Teil 1: Neue Rudistenfauna aus dem Maastrichtien von Maniago (Friaul) nebst stratigraphischem Anhang. *Archiv für Biontologie*, **5** (1; **1**): 68pp., 13 figs, atlas.

Kühn, O. 1932. Rudistae from Eastern Persia. *Records of the Geological Survey of India*, **66** (1): 151–179.

—— **& Pejović , D.** 1959. Zwei neue Rudisten aus Westserbien. *Sitzungsberichten der Österreichischen Akademie der Wissenschaften, Wien, Mathematisch-Naturwissenschaftliche Klasse*, (1) **168** (10): 979–989, pls 1–4.

Kutassy, A. 1934. Pachyodonta mesozoica. (Rudistis exclusis.). *Fossilium Catalogus*, 1, Animalia, **68**: 202pp. W. Junk, The Hague.

Lamarck, J. B. de 1801. *Système des animaux sans vertébrés*. viii + 432 pp. Paris.

MacGillavry, H. J. 1937. Geology of the Province of Camaguey, Cuba with revisional studies in rudist paleontology (mainly based upon collections from Cuba). *Physiographisch-Geologische Reeks der Geographische en Geologische Mededeelingen, Amsterdam*, **14**: 168pp., 10 pls.

Matheron, P. P. E. 1842–43. Catalogue methodique des fossiles des Bouches du Rhone. 8vo, Marseilles.

—— 1880. *Recherches Paleontologiques dans le midi de la France, ou étude sur les Animaux fossiles decouverts dans cette region* livres 1 – 7, 12 pp, 44 pls.

Milovanović, B. 1934. Les rudistes de la Yougoslavie. *Geoloski Anali Balkanskoga Paluostrva*, **12** (2): 275–308, pls 1–5.

—— 1935. Novi Rudisti Srbije. *Glasnik Srpske Kral'ev Akademije*, **166**: 47–125, 31 figs.

—— 1937. Les nouveaux rudistes de la Serbie. *Bulletin de l'Academie Royale de la Serbie, Academie des Sciences Mathematiques et Naturelles, (B) Sciences Naturelles*, 3: 42 pp., 31 figs.

Orbigny, A. D. d' 1847. Considerations zoologique et géologiques sur les Brachiopodes ou PalleoBranches (parts 1, 2). *Comptes Rendues Hebdominaires de l'Academie des Sciences, Paris*, **25** (5): 193–95; **26** (7): 266–69.

Palmer, R. H. 1933. Nuevos rudistas de Cuba. *Revista Agricultura, Havana*, **14**: 95–125, pls 1–10.

Pamouktchiev, A. M. 1967. Représentants Maestrichtiens du genre *Biradiolites* Orbigny de la Région Bresnik (Bulgarie de l'Ouest). *Annuaire de l'Université de Sofia, Faculté de Géologie et Géographie*, (1, Géologie) **60**: 31–73, pls 1–3.

—— 1975a. Origine et phylogénie du genre *Pironaea* (Hippuritidae, Maestrichtien) de l'Europe de Sud-Est et d'Asie Mineure. *Geologica Balcanica, Sofia*, **5** (2): 81–92.

—— 1975b. Espèces nouvelles de *Pironaea* (Hippuritidae). *Paleontology, Stratigraphy and Lithology, Sofia*, **3**: 19–26, pls 1–5.

—— 1979. Rudist fauna of the Maestrichtian in Bulgaria (the district of Breznik). III. *Annuaire de l'Université de Sofia 'Kliment Ohridski' Faculté de Géologie et Géographie*, (1, Géologie) **73**: 213–246.

Parona, C. F. 1900. Sopra alcune Rudiste senoniane dell'Appenino meridianale. *Memorie della Reale Accademia delle Scienze di Torino*, (2) **50**:

—— 1908. Fauna a rudiste della Pietra di Subiaco nella Valle dell'Aniene. *Bull. Soc. Geol. Italie*, **27**: 299–310, pl. 9.

Pejović , D. 1967. *Sabinia rtanjica* n. sp. iz mastrihta isto ne Srbije. *Vesnik Zavod za Geoloka i Geofizi ka Istra ivanja, Belgrade*, (A) **24–25**: 295–299, pls 1–2.

—— **& Radoičić , R.** 1987. Contribution to the study of Upper Cretaceous stratigraphy of Brač. *Geologija, Ljubljiana*, **29**: 121–150.

Philip, J. 1986. Étude paléontologique du genre *Sabinia* (Rudiste à canaux) des récifs du Campanien de Tunisie. *Géobios, Lyon*, **19** (2): 247–251, 1 pl.

—— **& Platel, J.-P.** 1987. Sur la presence du genre *Torreites* (rudiste de la province Caraïbe) dans le Campanien du Dhofar (sud de l'Oman): conséquences sur l'evolution paléobiogéographique du Pacifique et de l'océan Indien au Crétacé. *Compte Rendu Hebdomadaire des Séances de l'Academie des Sciences, Paris*, (2) **304** (12): 679–684.

—— **&** —— 1994. *Praetorreites*, nouveau genre de rudiste du Campanien d'Oman. *Géobios, Villeurbanne*, **27** (3): 303–319.

Pirona, G. A. 1868. Supra una nuova specie di *Hippurites*. *Atti della Societa italiana di scienze naturali, Milan*, **11**:

Pons, J. M., Schroeder, J. H., Hofling, R. & Moussavian, E. 1992. Upper Cretaceous rudist assemblages in Northern Somalia. *Geologica Romana*, **28**: 219–41.

Rojas, R., Iturralde-Vinent, M., & Skelton, P. W. (in press). Stratigraphy, composition and age of Cuban rudist-bearing deposits, Third International Conference on Rudists, Mexico City, 1993. *Revista del Instituto de Geologia de la Universidad Nacional Autonoma de Mexico.*

Ross, D. J. & Skelton P. W. 1993. Rudist formations of the Cretaceous; a palaeoecological, sedimentological and stratigraphical review. *Sedimentology Review*, no.1: 73–91. Blackwell Scientific Publications, Oxford.

Skelton, P. W. 1978. The evolution of functional design in rudists (Hippuritiacea) and its taxonomic implications. *Philosophical Transactions of the Royal Society of London*, B **284**: 305–318.

—— 1991. Morphogenetic versus environmental cues for adaptive radiations. *In*, Schmid-Kittler, N. & Vogel, K. *Constructional Morphology and Evolution*: 375–388. Springer Verlag, Stuttgart.

—— **& El-Asa'ad, G. M. A.** 1992. A new canaliculate rudist bivalve from the Aruma Formation of central Saudi Arabia. *Geologica Romana*, **28**: 105–117, 5 figs, 2 tab., 2 pls.

——**, Nolan, S. C. & Scott, R. W.** 1990. The Maastrichtian transgression onto the north-western flank of the Proto-Oman Mountains: sequences of rudist-bearing beach to open shelf facies. *In:* Robertson, A. H. F., Searle, M. P. and Ries, A. C. (eds). The Geology and Tectonics of the Oman Region. *Geological Society of London, Special Publication*, **49**: 521–547.

—— **& Wright, V. P.** 1987. A Caribbean rudist bivalve in Oman: island-hopping across the Pacific in the Late Cretaceous. *Palaeontology*, **30** (3): 505–529, pls 61–62.

Sladić-Trifunović, M. 1983a. *Branislavia*, a new rudist genus from Maastrichtian of Bačevića in east Serbia. *Annales Géologiques de la Péninsule Balkanique*, **45**: 207–216, pls 1–7.

—— 1983b. Paleontological characteristics and biostratigraphic significance of *Pseudopolyconites*. *Annales Géologiques de la Péninsule Balkanique*, **47**: 217–309, pls 1–48.

—— 1989. Pironaea-Pseudopolyconite Senonian of the Apulian Plate: palaeobiogeographic correlations and biostratigraphy. *Memorie della Società geologica Italiana*, **40**: 149–162, pls 1–5.

Swinburne, N. H. M. 1990. The extinction of the rudist bivalves. *Unpublished PhD thesis*. 175 pp. The Open University, Milton Keynes.

——**, Bilotte, M. & Pamouktchiev, A. M.** 1992. The stratigraphy of the Campanian-Maastrichtian rudis beds of Bulgaria and a reassessment of the range of the genus *Pironaea*. *Cretaceous Research*, **13**: 191–205, 7 figs.

Toucas, A. 1903–04. Études sur la classification et l'évolution des Hippurites.

Mémoire no. 30; Mémoires de la Société Géologique de France; Paléontologie, **11** (2) (1903): 1–64, pls 1–7 (7–13); **12** (4) (1904): 65–128, pls 8–17 (9–18).

—— 1907–09. Études sur la classification et l'évolution des Radiolitidés. *Mémoire no. 36; Mémoires de la Société Géologique de France; Paléontologie*, **14** (4) (1907): 1–46, pls 1–8 (11–18); **16** (1) (1908): 47–78, pls 9–15 (1–7); **17** (1) (1909): 79–132, pls 16–24 (1–9).

Vautrin, H. 1933. Sur quelques formes nouvelles de rudistes recueillis en Syrie Septentrionale. *Notes et Memoires de la Haute Commissariat de la Syrie et du Liban, Republique Française*, **1**: 29–43, pls 1–5.

Vogel, K. 1970. Die Radioliten-Gattung *Osculigera* Kühn (höhere Oberkreide) und die Funktion kennzeichnender morphologischer Eigenschaften der Rudisten. *Paläontologische Zeitschrift, Stuttgart*, **44** (1–2): 63–81, pls 6–8, 6 figs.

Woodward, S. P. 1855. On the structure and affinities of the Hippuritidae. *Quarterly Journal of the Geological Society*, **11**: 40–61, pls 3–5.

Zittel, K. A. 1865–66. Die Bivalven der Gosaugebilde in den nordostichen Alpen Beitrag zur Characteristik der Kreideformation in Osterreich. *Denkschriften der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Wissenschaftliche Klasse, Wien*, **24** (2) & **25** (2), 293pp. 27 pls.

—— 1881–85. *Handbuch der Palaeontologie 2. Mollusca und Arthropoda.* 900pp., 719 figs. Munchen und Leipzig.

Note added in proof: One of us (PWS) has recently had the opportunity to see some specimens of *Durania mutabilis* (Stoliczka, 1871) collected from the Maastrichtian of southern India by Professor Malcolm Hart. It is clear that the material described above (p. 296) as *Durania* cf. *gaensis* (Dacqué, 1903) can be attributed to *D. mutabilis*. Whether *D. gaensis* and *D. mutabilis* (which has priority) should be considered to be synonyms remains to be resolved.